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FOOD AND COVER OF FLUCTUATING POPULATIONS  
OF NORTHERN CRICETIDS

by



GERALD ROY DYKE

A THESIS

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The undersigned certify that they have read,  
and recommend to the Faculty of Graduate Studies for  
acceptance, a thesis entitled "Food and Cover of  
Fluctuating Populations of Northern Cricetids" submitted  
by Gerald Roy Dyke in partial fulfilment of the require-  
ments for the degree of Doctor of Philosophy.

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"They have one obvious part to play, that of turning grass into flesh, in order that carnivorous Goths and Vandals may subsist also, and in their turn proclaim, 'All flesh is grass'."

— Elliot Coues



## ABSTRACT

The trophic niches of *Peromyscus maniculatus*, *Clethrionomys rutilus* and *C. gapperi* were analyzed during 1965-68 in taiga southwest of Great Slave Lake through examination of stomach contents and by laboratory tests for preference, weight maintenance and consumption rates. A new method for determining preference is described.

Both genera are frugivorous and eat a few kinds of fruits in large quantities. Fruits that overwinter on the plant are important in winter and early summer when the more ephemeral ones are not available. In addition, *P. maniculatus* was found to be partly insectivorous whereas *Clethrionomys* spp. ate large quantities of mushrooms, chlorophyllous material and arboreal lichens. Food habits reflected seasonal availability.

Records of phenology, vegetative and fruit production, aspects of cover, and rodent density were kept for the four years in eleven plant associations representing six of the most common faciations of the area. Five of these associations were represented on each side of the Kakisa River which marks the boundary between the ranges of *C. rutilus* and *C. gapperi*; and one was only represented in *C. rutilus* range. *P. maniculatus* was found throughout the study area.

The three rodents reached a peak in 1966, but in 1967, while *C. rutilus* continued to increase, *P. maniculatus* and *C. gapperi* declined. All species declined in 1968.

Delayed phenology and reduced fruit production in 1967 and, to a lesser extent, in 1968 is attributed to cold spring weather with a persisting snow cover. A large mushroom crop in 1967, and a slightly smaller one in 1968, were probably caused by high rainfall in those summers. Such variations were reflected in stomach contents.





The effect of weather on production of overwintering fruits is carried over to the following spring. Thus, the bumper crop of 1966 gave rise to an abundance of overwintered fruits in the otherwise unfavorable spring of 1967. However, only *C. rutilus* appeared to benefit from this food source that year. The decline in all populations in 1967-68 may have been abetted by a scarcity of overwintered fruits following the poor crop produced in the cold wet summer of 1967.

Biologically, rodent numbers were not correlated with preferred foods. The data imply that such spatial dependence is overcome by mobility in *P. maniculatus* and opportunism in *Clethrionomys* spp. Correlations were shown with cover, however—fallen trees in *P. maniculatus* and foliage cover in *Clethrionomys* spp. Seasonal and yearly variation in faunal composition of the various plant communities indicated that *P. maniculatus* satisfied their habitat requirements at the expense of *Clethrionomys* spp. Similarity of food and cover niche requirements is submitted to explain separation of the ranges of *C. rutilus* and *C. gapperi*.

The results of the study are related to specific and general population theory.



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## INTRODUCTION

Viewed at a point in time, the most obvious features of the biosphere, save the great variety in its members and the vastness of their numbers, are the patterns of distribution and density of its component species. Spatial variations in density are too numerous to cite but seem to exist for all organisms, none being homogeneously spread throughout the biosphere.

In addition, numbers vary temporally. The bulk of reports concerning multiannual population fluctuations of animals appeared around 1930. These led Elton (1950), who was cognizant of the ideas of Spencer (1863) and the mathematical theses of Lotka (1925) and Volterra (1931), to state that "one of the most important generalizations that can be made about wild animal populations is that they fluctuate greatly in numbers." This generalization is supported by many population ecologists (e.g. Smith, 1935; Lack, 1954a; Andrewartha, 1961; Cockrum, 1962; Ehrlich and Birch, 1967), but is denied by Slobodkin (1961).

There is interspecific variability in the amplitude and frequency of population fluctuations. For example, short-tailed shrews (*Blarina brevicauda*) undergo less than a fourfold change in numbers (Terman, 1966), whereas the lasiocampid moth (*Dendrolimus pini*) may increase its numbers by a factor of 10,000 (Schwerdtfeger, 1941). The mean period of number changes in Indian elephants (*Elephas maximus*) is 70 to 100 years (Casserby, 1924), but only 3 to 5 years in certain rodents such as those of the present study.

A relative lack of extinctions and eruptions in these temporal changes has been used as an argument for density-dependent control of numbers (Nicholson, 1933; Hairston, Smith and Slobodkin, 1960; Slobodkin, 1961).







In reality, however, few species escape extinction (Simpson, 1952) and eruptions *are* plentiful, albeit seemingly overemphasized by the literature. In the spatial aspect of numbers tremendous variation is also evident. The alternative to constancy thus appears to be the case—Birch (1953) even found fluctuations in experimentally-constant environments. In any event it is still necessary to seek explanations for changes in numbers.

The spatial aspect of animal numbers has caused less controversy than the temporal aspect for which many explanations have been presented. Later workers are more given to comprehensive theories of population "control" than earlier ones (Solomon, 1949), but there is still a general tendency to espouse a single environmental attribute or mechanism thereof. Among the schools of explanation are those that attribute number fluctuations to weather (Elton, 1924, 1927 and 1929; Uvarov, 1931), food (Braestrup, 1940; Lack, 1954a; Pitelka, 1958), predation (Errington, 1967), parasitism (Erickson, 1944), disease (Krebs, 1966; DeLong, 1967) and social factors (Christian, 1955). Of note are the three great types of opposing schools: extrinsic (Thompson, 1955) versus intrinsic (Chitty, 1952 and 1960; Christian, 1961; Wynne-Edwards, 1962; Christian and Davis, 1964); biotic (Escherich, 1924) versus abiotic (Bodenheimer, 1930); and density-dependent (Grinnel, 1904; MacLagan, 1932; Nicholson, 1933; Lack, 1954a) versus density-independent (Andrewartha and Birch, 1954). The latter controversy parallels that of the presence (Nicholson, 1933; Elton, 1949) or absence (Ehrlich and Birch, 1967) of a "balance" in nature.

These various schools, by producing evidence to support a particular factor or group of factors, collectively strengthen my contention that numbers have to be explained, not only by interacting environmental components, but by different components playing major roles at different



times and places in different species and populations. Two interacting factors, at least, have been found to explain numbers; for example: the sporozoan parasite *Adelina tribolii* and food in *Tribolium castaneum* (Park, 1948); food shortage and strongylosis in a declining population of red grouse (*Lagopus scoticus*) (Lovat, 1911); and food shortage and severe weather in *Microtus* (F. Frank, 1957). Again, Holdaway (1932) attributed population control in *Tribolium confusum* to intraspecific interactions, but the level at which that control kept the population was determined by a physical factor (moisture). Food is likely to play a major role in open, cultivated areas (witness the vole plagues of Europe); weather is probably a paramount factor in boreal regions where snow is present for most of the year (Formozov, 1946; Fuller, 1967; Fuller, Stebbins and Dyke, 1969); intrinsic factors may be expected to have a great influence in confined populations such as those studied by Retzlaff (1938), Calhoun (1952), Strecker and Emlen (1953), Clarke (1955), Christian (1955), Southwick (1955a and b), Crowcroft and Rowe (1957) and Lloyd and Christian (1967).

That the solution to problems of density variation is not simple has been realized almost since the inception of population ecology, as exemplified by the following quotations:

There appears to be no adequate basis for the idea that the same single factor governs the distribution of most animals. Such a conclusion probably results from leaving the organism out of consideration (Shelford, 1911).

The density of a population under natural conditions is determined by the interaction of almost countless forces, continually varying in intensity, the effect of each force influencing in some degree the effect of every other force (Smith, 1935).

Cyclic phenomena present themselves—as do other biological problems—as an interaction between biological events and environmental factors of a particularly complicated structure, depending



on several factor groups and many individual factors (F. Frank, 1957).

It is of course understood that both extrinsic and intrinsic factors influence all fluctuations; the fundamental problem is to evaluate the importance of each, or at least to determine which is the major cause of variation in specific cases (Odum, 1959).

It is not possible at the moment to say what proportion of the total population fluctuations occurring in nature is intrinsic, and what proportion is due to the environment. Any attempt to try to attribute major importance to one factor or the other is probably premature (Slobodkin, 1961).

If we can draw any general conclusions from the work which has been done in natural populations, it is that single, neat "control" mechanisms are unlikely to explain fluctuations in the size of single populations let alone numbers of all organisms of a trophic level (Ehrlich and Birch, 1967).

Finally, in discussing the populations to be treated presently, Fuller (1969a) stated:

...the present findings...cast doubt on the idea that all population control can be reduced to the same set of rules.

For the present study the premise that complexly-interrelated environmental components influence population densities is accepted. The study is, therefore, limited in scope to an evaluation of the influence of food and cover, over a period of four years, on the numbers of *Peromyscus maniculatus borealis*, *Clethrionomys rutilus dawsoni* and *C. gapperi athabasca* in an area of taiga in the southern Mackenzie district. Reference will be occasionally made to other factors when their importance is indicated.

Despite the ecological and scientific importance of these animals (they are now used extensively in the investigations of population phenomena), little is known of their natural history, especially food habits. Although this lack of knowledge handicaps ecological investigations on the whole (Engelmann, 1966; Fleharty, 1969) it is especially obvious





in the study of boreal rodents in North America. This dearth is partly explained by the secretive habits and extreme pulverization of food by the rodents, and an avoidance of northern regions by scientists. Thus, the first purpose of this study was an attempt to determine the trophic niches of these three species. I believe that such a study is necessary for an eventual comprehension of the community and ecosystem.

The second purpose of the study was to examine the environment in an attempt to explain temporal and spatial differences in the densities of the animals.





## THE ANIMALS

The subjects of these investigations (Fig. 1) belong to two species of Microtinae, *C. rutilus* and *C. gapperi* (red-backed voles); and one of Cricetinae, *P. maniculatus* (deermice). *C. rutilus*, common in northern Russia, occurs only in Alaska, northern British Columbia and the two Canadian Territories, while *C. gapperi* occupies the rest of Canada and the northern United States, extending southward along the mountain systems (Walker *et al.*, 1964; Burt and Grossenheider, 1964; Hall and Kelson, 1959). These species are apparently completely allopatric (Rand, 1944; MacPherson, 1965). Like *C. gapperi*, *P. maniculatus* is confined to North America. Here it is found everywhere except on the northern and southern borders of the continent.

These animals exhibit marked numerical changes over relatively short periods, are generally easily caught and handled, and their rapid generation replacement minimizes the lag between cause and effect (population changes). Thus, they are well suited to population studies.

Adaptations for acquiring, ingesting and assimilating food contribute considerably to an animal's total morphology. Consequently, within uniform taxonomic groups such as the class Mammalia, structural variations in appropriate organs and systems are generally reflections of dietary variations. Together with some knowledge of behavior, these morphological reflections have classically led to speculation about food habits in the absence of actual knowledge. Figure 1 compares *Peromyscus* and *Clethrionomys* for this purpose.

Examination of the external morphology discloses that, of the two genera, *Peromyscus* has larger eyes, possibly an adaptation for nocturnal vision; larger ears which may make for more efficient collection of sound





Figure 1. Comparisons of morphological characters reflecting food habits in the two genera studied. Abbreviations: *ca*, caecum; *co*, colon; *es*, esophagus; *gs*, glandular part of stomach; *si*, small intestine.

PEROMYSCUS MANICULATUS

CLETHRIONOMYS SPP.

EXTERNAL  
MORPHOLOGY



UPPER LEFT  
MOLARS



Crown view



Crown

Labial

DIGESTIVE  
TRACT







from moving prey; longer legs which are also better adapted for leaping, as was seen in the laboratory; a longer tail which might be more valuable as a balancing organ; and a more laterally compressed trunk characteristic of fast moving animals. These features suggest predation in *P. maniculatus* but not in *Clethrionomys* spp.

The teeth of *P. maniculatus* are brachybunodontic while those of *Clethrionomys* spp. are hypsoselenodontic or hypsolophodontic. Omnivory is therefore indicated for the former, and a diet of fibrous vegetation for the latter.

The stomachs of both genera are similar on superficial examination. Since mice and voles are roughly similar in total body size, the lengths of their digestive tracts may be compared directly. That of *P. maniculatus* is shorter, particularly the caecum, suggesting carnivory or, at least, omnivory; the long gut and caecum of *Clethrionomys* spp. suggests a diet containing more cellulose than that of *P. maniculatus*.

Behaviorally, the deermouse is the more agile of the animals (personal observation), and is nocturnal as opposed to the voles which are active at short intervals, especially during the day (Stebbins, 1968; also see food-preference tests discussed subsequently). *P. maniculatus* also may have a larger home range than *Clethrionomys* spp. (Beer, 1961; Burt and Grossenheider, 1964). As a general rule, carnivorous small mammals have a larger home range than herbivorous ones (Blair, 1940 and 1943; Cockrum, 1962). If we may neglect other variables affecting range size—body size, habitat selection, mobility, and population density (Cockrum, *op. cit.*)—in these populations, the difference must be due to difference in food habits. Such circumstantial clues strengthen the case





for carnivory in deermice and not in the red-backed vole.

The behavioural characteristic of winter torpidity in deermice (Stebbins, 1968) might indicate a food lack at that time of year and a possible dependency on ephemeral foods such as fruits and insects. Voles, which do not exhibit torpidity, may eat foods that are constantly available, such as vegetative parts of plants.

The ranges of the two species of *Clethrionomys* do not overlap in my study area, nor along the Alaska Highway (Rand, 1944). Since these animals seemingly occur in similar environments, mutual exclusion through competition because of similar trophic niches may explain this phenomenon.

Synoptically, *P. maniculatus* is likely an insectivore with some probability of omnivory. Fruits may form the herbivorous part of its diet. (It is more common, considering the dental pattern alone, to attribute only spermivory to this species.) The two species of *Clethrionomys*, on the other hand, may be predicted to have similar diets consisting of less nutritious vegetative parts of plants.

Such speculations about food niches are common, but are inherently crude and uncertain. These conclusions were tested in the current study through an examination of food preference and of natural consumption.



## THE STUDY AREA

Field studies and collections, and some experiments, for this inquiry were conducted from 1965 to 1968 near the northern limit of the continuous taiga southwest of Great Slave Lake, N.W.T. The area (Fig. 2) was so chosen that populations of both *C. rutilus* and *C. gapperi* could be examined simultaneously, since their ranges meet at the Kakisa River. The Heart Lake Biological Station of the University of Alberta served as a base of operations.

The total number of native and naturalized seed plants in the southern Mackenzie region is 558 (Thieret, 1963a). Since the majority of these inhabit clearings, the use of forested study areas reduced this number to a manageable size.

### Community Descriptions

Areas containing representative plant communities were selected along 60 miles of the Mackenzie and Great Slave Lake Highways. The demands of *homogeneity* (to insure reliability of samples) and *expanse* (to minimize the effects of transient animals on population indices) precluded mixed and small stands. Of the sufficiently large pure associations it was possible to find white spruce (*Picea glauca*), poplar (*Populus tremuloides*), immature black spruce (*Picea mariana*), jackpine-juniper (*Pinus banksiana*—*Juniperus communis*) and parklike jackpine on both sides of the Kakisa River. No mature black spruce forest, however, could be found in *C. gapperi* territory. Figure 2 shows the positions of the 11 areas described below.

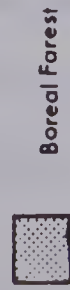
White spruce. In spite of its potential (Moss, 1955) and actual dominance throughout most of the "Mackenzie basin" (Raup, 1936), white spruce was scarcer than jackpine or black spruce in the study area, and



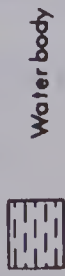


Figure 2. Location of the study area and plant associations examined.  
The Kakisa River serves as a boundary between the two  
species of *Clethrionomys*.





Boreal Forest



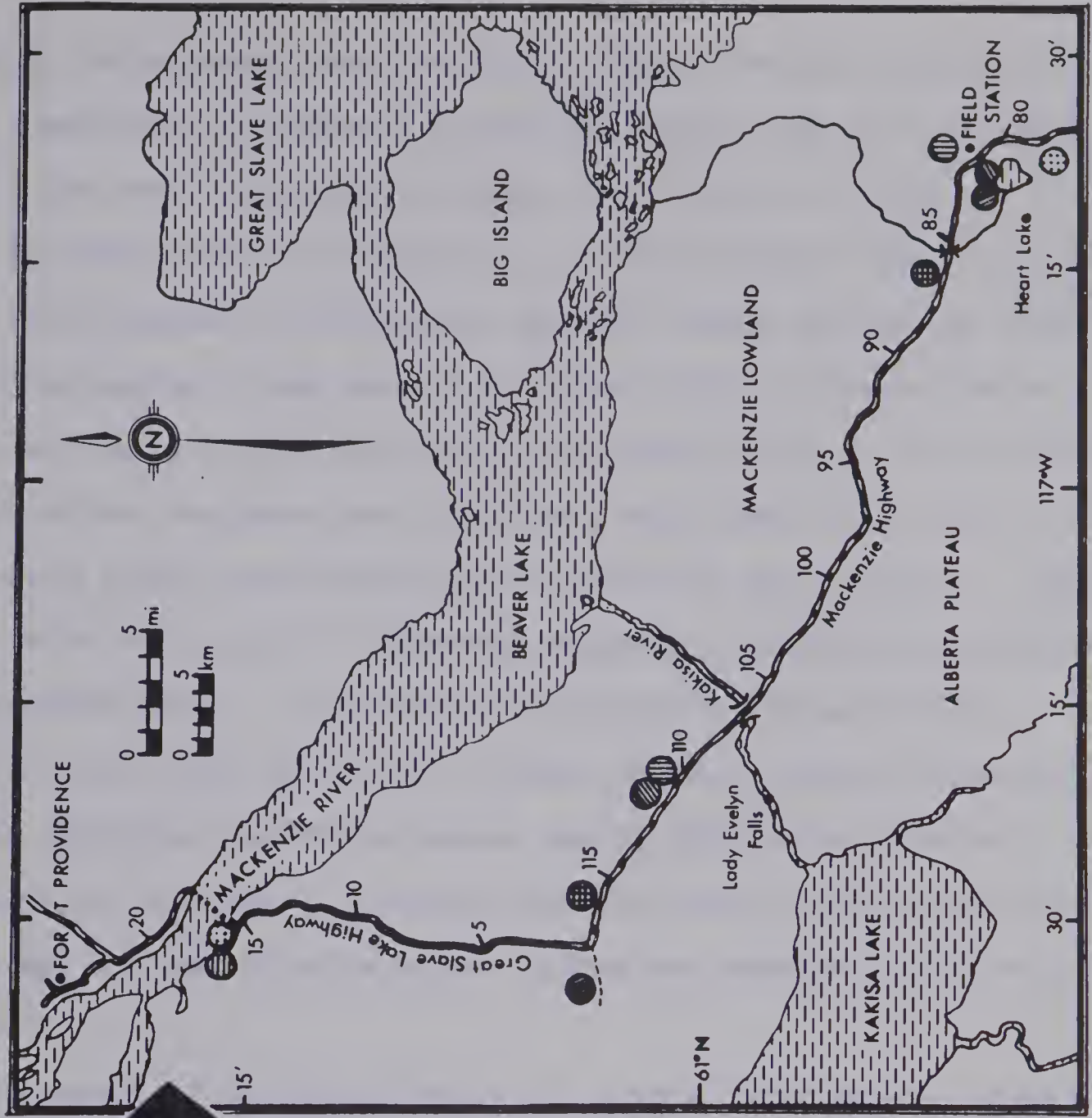
Water body



Highway with milepost

#### VEGETATION COMMUNITIES STUDIED

- WHITE SPRUCE
- POPLAR
- IMMATURE BLACK SPRUCE
- MATURE BLACK SPRUCE
- JACKPINE-JUNIPER
- PARKLIKE JACKPINE







monotypic white spruce stands were rare. Thus it was not possible to find this community in a comparable successional stage in the two vole territories that were in reasonable proximity for purposes of study.

The white spruce association in *C. rutilus* territory (Fig. 3) was the only site situated in the Mackenzie Lowlands (Camsell and Malcolm, 1921). The stand covered a large area of the alluvial flats of the Mackenzie River and may be classified as flood plain spruce (Raup, 1933 and 1946) or the shrub-herb faciation (Moss, 1953) of a white spruce association. The understory plants were typically few in number but not in species. These were mainly *Rosa woodsii*\*, *Shepherdia canadensis*, *Epilobium angustifolium* and *Viburnum edule*. The ground cover consisted of *Linnaea borealis*, *Mitella nuda*, *Cornus canadensis*, *Geocaulon lividum*, *Fragaria virginiana*, *Pyrola asarifolia*, and feather mosses (chiefly *Hylocomium splendens*). Aspen poplar was sparsely scattered throughout the faciation as were its seedlings and those of white spruce. Litter was prevalent on the forest floor.

Southeast of the Kakisa River, in *C. gapperi* territory, the stand studied (Fig. 4) may be regarded as upland mesophytic spruce (Raup, 1933 and 1946) or a feather moss faciation (Moss, 1953). This drier, more heavily canopied community is the association climax of its counterpart in *C. rutilus* territory. Because of the characteristically dense overstory and subsequent shade (Thieret, 1964) the shrub and herb strata were almost nonexistent, and the ground cover consisted essentially of a continuous thick carpet of feather mosses. The elements that did exist were those

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\**R. acicularis* and hybrids were also likely present on the study area.





Figure 3. White spruce association in *C. rutilus* area.











Figure 4. White spruce association in *C. gapperi* area.







also found in the shrub-herb faciation of *C. rutilus* territory. Leaf litter was much less common than in its counterpart.

The parklike white spruce of Raup (1946) was not present in the study area.

Poplar. In spite of the scarcity of aspen poplar, two stands were found—one on each side of the Kakisa River. Because of white spruce ecesis and the presence of elements of the surrounding jackpine forest which the poplar succeeded, neither of these stands were pure. However, they both shared the dense understory, copious leaf litter and dry habitat characteristic of the poplar community. Also, the topsoil in these associations was deeper than in the surrounding jackpine areas, possibly explaining the presence of the poplars.

The associated flora of the stand northwest of the Kakisa River (Fig. 5) contained *R. woodsii*, *S. canadensis*, and *V. edule* in the understory, and *L. borealis*, graminoids and *G. lividum* in the ground cover. Feather mosses were lacking as is characteristic of this type of forest (La Roi, 1967). A unique feature of the community was a distinct substratum formed by the invading white spruce. This site was only about two acres in area and was the smallest of the habitats studied.

The other poplar stand (Fig. 6), which was probably older, was of similar composition but differed in that shrubby and herbaceous vegetation was more profuse. It also had fewer fallen trees.

Although poplar communities differed from those dominated by white spruce in that their canopies (especially after abscission) were much less effective in excluding precipitation and radiation, the composition of the understories of both was similar.







Figure 5. Poplar association in *C. rutilus* area.









Figure 6. Poplar association in *C. gapperi* area. Note the dense understory mainly composed of *Shepherdia canadensis*.







Immature black spruce. Open bogs and tamarack (*Larix laricina*) associations, which are related to this category, were scarce in the area. These proved to be devoid of a cricetid fauna possibly because of their extreme wetness. For this reason also they could not be trapped expeditiously and are omitted from this study. Tamarack associations, save for an abundance of water, were floristically and ecologically similar to the black spruce-peat moss (*P. mariana*—*Sphagnum*) association (Moss, 1955) considered here.

The immature black spruce community, variously named (Lewis and Moss, 1928; Raup, 1946; Moss, 1955), is the common muskeg composed of *Sphagnum* spp. and a great variety of shrubs, herbs and fruticose lichens. Chief among these were *Vaccinium vitis-idaea*, *Ledum groenlandicum*, *Empetrum nigrum*, *Cladonia* spp. and grasses. Since this type of vegetation was the most common in the area, two remarkably similar sites could be chosen for study (Figs. 7 and 8). In these sites tamarack and bog birch (*Betula glandulosa*) were common and, to a lesser extent, so were black spruce seedlings. Lack of foliage cover, fallen trees, and litter was obvious as was also the abundance of plant species.

Mature black spruce. The immature black spruce forest is regarded as a subclimax community (Moss, 1955) of a sere terminating in a mature black spruce community. This edaphic climax (Moss, 1953), also bearing several names (Lewis and Moss, 1928; Raup, 1946; Moss, 1953), differed in the present study area from the immature stage in that it was drier, and occupied more level terrain; and feather mosses had succeeded the *Sphagnum* series. In addition, the number of species present was much lower.

Unfortunately, only one stand was found in the study area, and that at the extreme northwest end of *C. rutilus* territory. As seen from





Figure 7. Immature black spruce association in *C. rutilus* area.



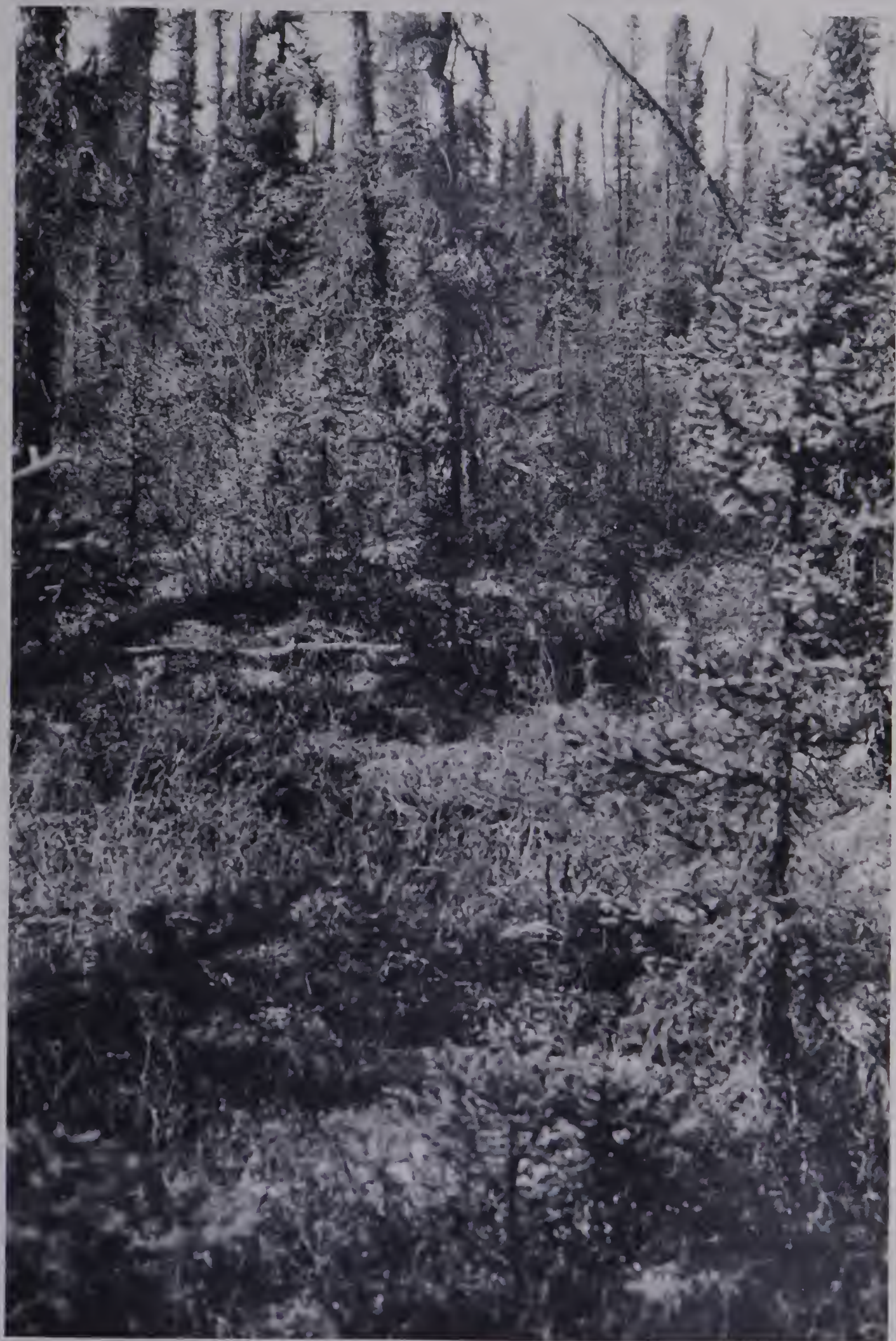






Figure 8. Immature black spruce association in *C. gapperi* area.  
Note the striking similarity to its counterpart in  
*C. rutilus* territory.









Figures 9 and 10 the understory was dense and composed almost exclusively of *L. groenlandicum*. The ground cover had a greater frequency of *V. vitis-idaea* than the immature stage, and *Peltigera* spp. and feather mosses had invaded. Foliage cover was the highest of the entire area, and litter and fallen trees were only slightly more plentiful than in muskeg.

Jackpine-juniper. Jackpine, the only pine species in the region, rivals black spruce in prevalence. It is found, along with its subsidiary flora, on dry, sandy sites, where it is admirably suited to the shallow soil covering the limestone bedrock which underlies much of the study area.

The pine-feather moss and pine-heath faciations of Moss (1955) were not recognizably distinct. However, an association, somewhat like the rocky pine woods of Raup (1946), which I call "jackpine-juniper," was studied because of its commonness and distinctness. The most obvious feature of this type of vegetation was the low substratum of *Juniperus communis* associated with the relatively young jackpine.

The two sites (Figs. 11 and 12) possessed, in addition to the characteristic juniper understory, a large number of associated elements, with pine and white spruce seedlings, *S. canadensis*, *Arctostaphylos uva-ursi* and *Cladonia* spp. being the most conspicuous. The slightly older stand in *C. gapperi* territory, however, had a less diverse flora offering less foliage cover as well as fewer fallen trees.

Parklike-jackpine. Parklike jackpine (Raup, 1946) consisted almost entirely of the dominant tree and ground cover, representing a more mature stage of the jackpine-juniper forest. But because of setbacks to succession possibly caused by burning, these stands were fairly scarce.

The two stands studied (Figs. 13 and 14) were very similar. Since







Figure 9. Mature black spruce in *C. rutilus* area, the only one of its kind in the study area.







Figure 10. *Ledum groenlandicum* which forms the understory in mature black spruce.











Figure 11. Jackpine-juniper association in *C. rutilus* area.









Figure 12. Jackpine-juniper association in *C. gapperi* area. Note the distinct stratum of *Juniperus communis*.









Figure 13. Parklike jackpine in *C. rutilus* area.



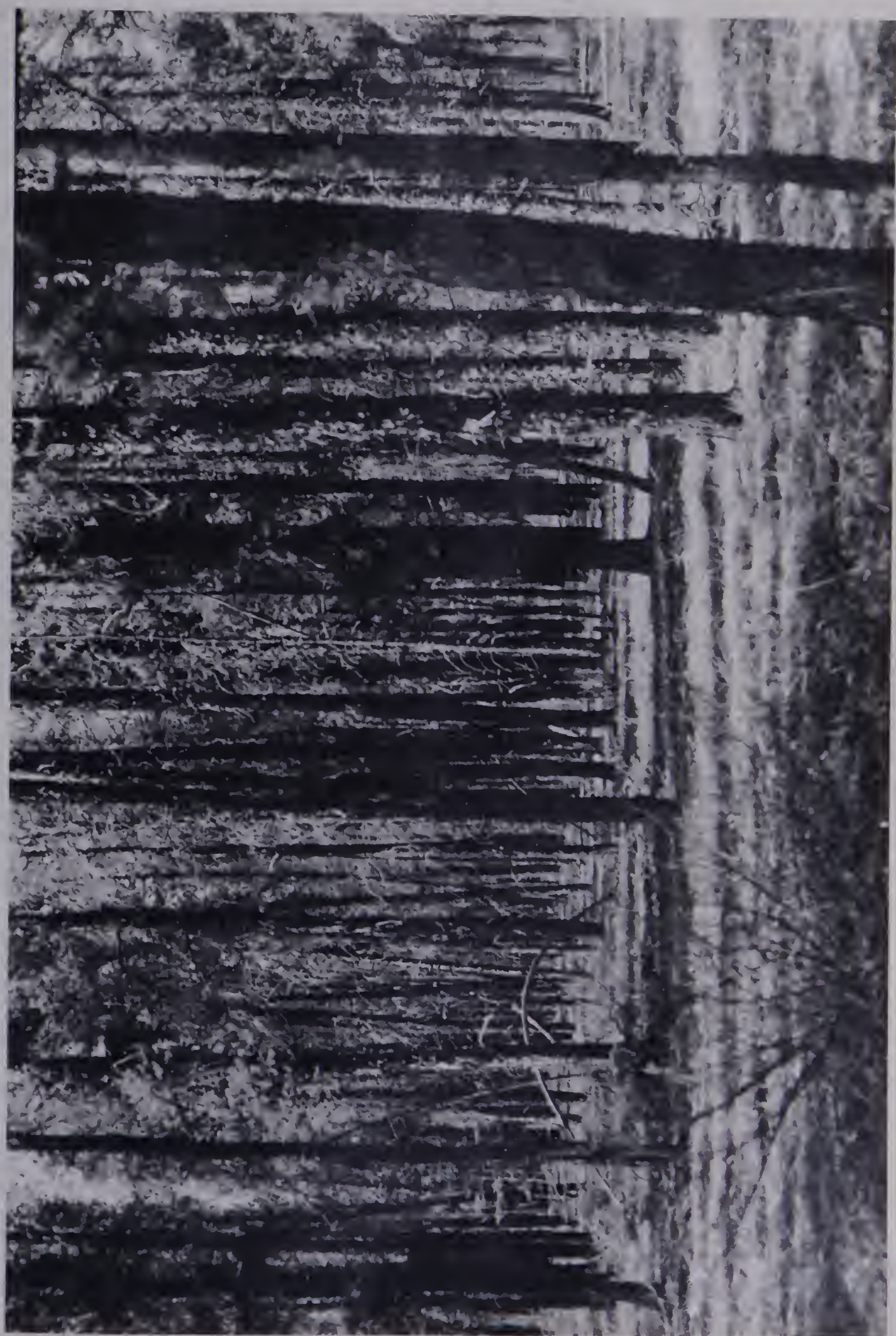








Figure 14. Parklike jackpine in *C. gapperi* area. At this stage of the sere practically all of the understory has disappeared.







the one in *C. rutilus* territory was successional younger, there were perceptibly more individuals of few species (*R. woodsii*, *S. canadensis*, and *V. edule*) present in the understory. The ground cover consisted almost entirely of *Cladonia* spp. and *A. uva-ursi*. Litter was almost as scarce as in muskegs, and foliage cover and fallen logs were virtually nonexistent.

### Climatic Difference in Habitats

Differential persistence of the winter snow cover, and variations in light, temperature and moisture are, to some degree, results of community structure, and can effect a broad spectrum of consequences on the subsidiary flora as well as directly on the rodent faunas. Table 1 contains measurements of the dominants in the communities studied. The type and spacing of these trees vary greatly and create distinctive conditions in the forests.

Open forests such as immature black spruce may accumulate more snow during winter and lose it earlier in spring than close-canopied forests like white spruce. Thus, the first snowfall of 1966 was seen to leave 2 cm of snow on the clearings and muskegs, almost as much in the jackpine forests, tiny patches in the poplar stands and none in the white spruce. Fuller, Stebbins and Dyke (1969) recorded the thickest snow cover in 1965-66 on Plot III, an immature black spruce forest, and the thinnest one in 1966-67 on Plot VI, a floodplain white spruce forest. Other plots, which were in mixed forests (Fuller, 1969a) had thinner snow covers in both winters than the more open area at the field station where depths were also measured. At the beginning of December, 1966, I noted that, while the snow cover was on the average 30 to 40 cm in depth, the muskegs





Table 1. Measurements of size and density of dominant and associated trees of vegetation communities studied.  
 All values are averages of 20 estimates. pt=*Populus tremuloides*, pg=*Picea glauca*, bg=*Betula glandulosa*, ll=*Larix laricina*, pb=*Pinus banksiana*, pba=*Populus balsamifera*.

Feature	White spruce	Poplar	Immature black spruce	Mature black spruce	Jackpine-juniper	Parklike jackpine
<i>C. rutilus</i> territory						
Height of dominant (m)	18	14	7	9	13	15
Dbh of dominant (mm)	127	101	76	103	125	127
Spacing of dominant (m)	2.0	1.5	3.9	3.6	3.3	3.4
Associated trees	pt	pg	bg	pg	nil	pg
			ll	ll		
				bg		
Height of associated trees (m)	17.0	9.0	1.5	4.8		1.8
			1.5	4.5		
				2.4		
Spacing of associated trees (m)	75	4.5	5.6	3.0		240
			6.0	3.0		
				12.0		
<i>C. gapperi</i> territory						
Height of dominant (m)	15	16	6		11	14
Dbh of dominant (mm)	102	127	76		125	177
Spacing of dominant (m)	1.2	1.8	3.0		2.3	3.1
Associated trees	nil	pg	pg		pba	nil
		pb	ll		pg	
Height of associated trees (m)		15	1.2		8	
		15	6		1.2	
Spacing of associated trees (m)		90	18		50	29
		180	150		18	



were covered with 60 cm and the white spruce of *C. gapperi* territory (the most densely-forested and heavily-canopied stand in the study area) had little more than 20 cm (falling qali increases the density rather than the depth).

At the end of the winter of 1966-67, snow left the roadside verges and clearings first. By the end of the first week in May only approximately one-fifth of the forest floor remained snow-covered in parklike jackpine; white spruce stands were fully covered except for the qamaniqs; mature black spruce, aspen poplar (leafless during both accumulation and ablation of snow) and jackpine-juniper were roughly two-thirds covered. The immature black spruce areas were still half-covered, probably because of their dense understories.

Accumulation of melt water also varied spatially. Except for the immature muskegs the only site where puddles were observed each spring was the white spruce stand in the *C. rutilus* area. The mature muskeg was perhaps damper than the remaining sites. These phenomena are probably more a result of physiographic and edaphic factors than of the vegetation.

No attempt was made to measure the radiation, temperature or humidity in the different forests, although some differences were qualitatively obvious. White spruce forests, especially the upland one in *C. gapperi* territory, appears to be darkest, coolest and most humid. In more open stands the lower strata are important determinants of the amount of light reaching the forest floor (compare Figs. 13 and 14 to Fig. 10). Variations in incoming radiation result also in temperature differences, but there is no direct correlation with humidity because of differences in drainage. Thus, though they are structurally similar, jackpine-juniper areas are drier than muskegs. Parklike jackpine areas are driest of all



because of good drainage and their open structure.

### General Weather Conditions

The mean daily maximum and minimum temperatures for the study area are presented by bi-monthly intervals in Figure 15 for the four summer months of the four years of the study. These records were made available by Mr. William Clark of the Mackenzie Forest Service at Heart Lake Tower, 100 m east of the field laboratory. They are supplemented by values from the thermistors of the biological station for early May, 1966 and 1967 and from the meteorological station at Hay River, N.W.T. for early May of 1965 and late May of 1967. The modifying influence of the Great Slave Lake on the Hay River temperatures was discussed by Fuller (1969a).

The coldest of the early spring periods occurred in 1967; the second coldest in 1968. The most obvious spring difference between 1965 and 1966 was the high minimum in the first part of May, 1966. For the remainder of the summer, 1967 and 1968 had lower temperatures than the other two years, but in August only 1968 was noticeably colder than the rest. The summers of 1965 and 1966 were not consistently different in temperature.

Figure 16 shows bi-monthly precipitation in the study area. These records were also obtained from the Heart Lake Fire Tower, but values for May, 1967 and the last half of August, 1968 are from the nearest official meteorological station at Hay River.

The wettest of the two summers, 1967 and 1968, surpassed the Hay River precipitation normal of 103.1 mm by about 70 and 35 mm respectively, while the two earlier summers were close to normal. For May also, precipitation was highest in 1967 followed by that of 1968. The value at that







Figure 15. Mean daily maximum (upper) and minimum (lower) temperatures in the study area during 1965-1968. Stippled bars refer to the first half (1-15) of each month and the open bars to the second half. The horizontal lines represent the 30-year climatic normals (Thompson, 1962) for Hay River, N.W.T., which area is probably slightly cooler than the study area (Fuller, 1969a). Arrows indicate a downward bias in the data caused by instrumental limitation.

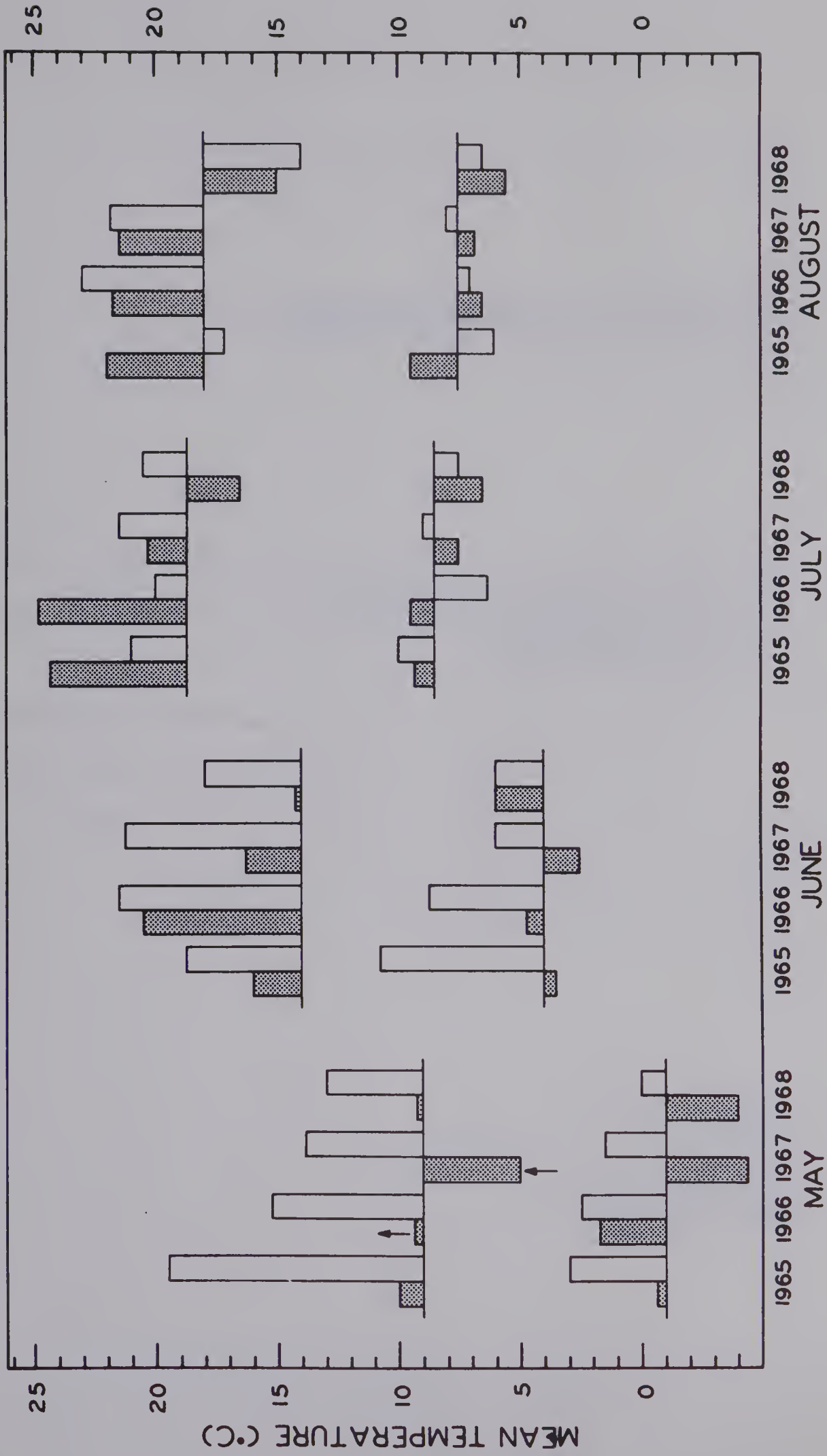
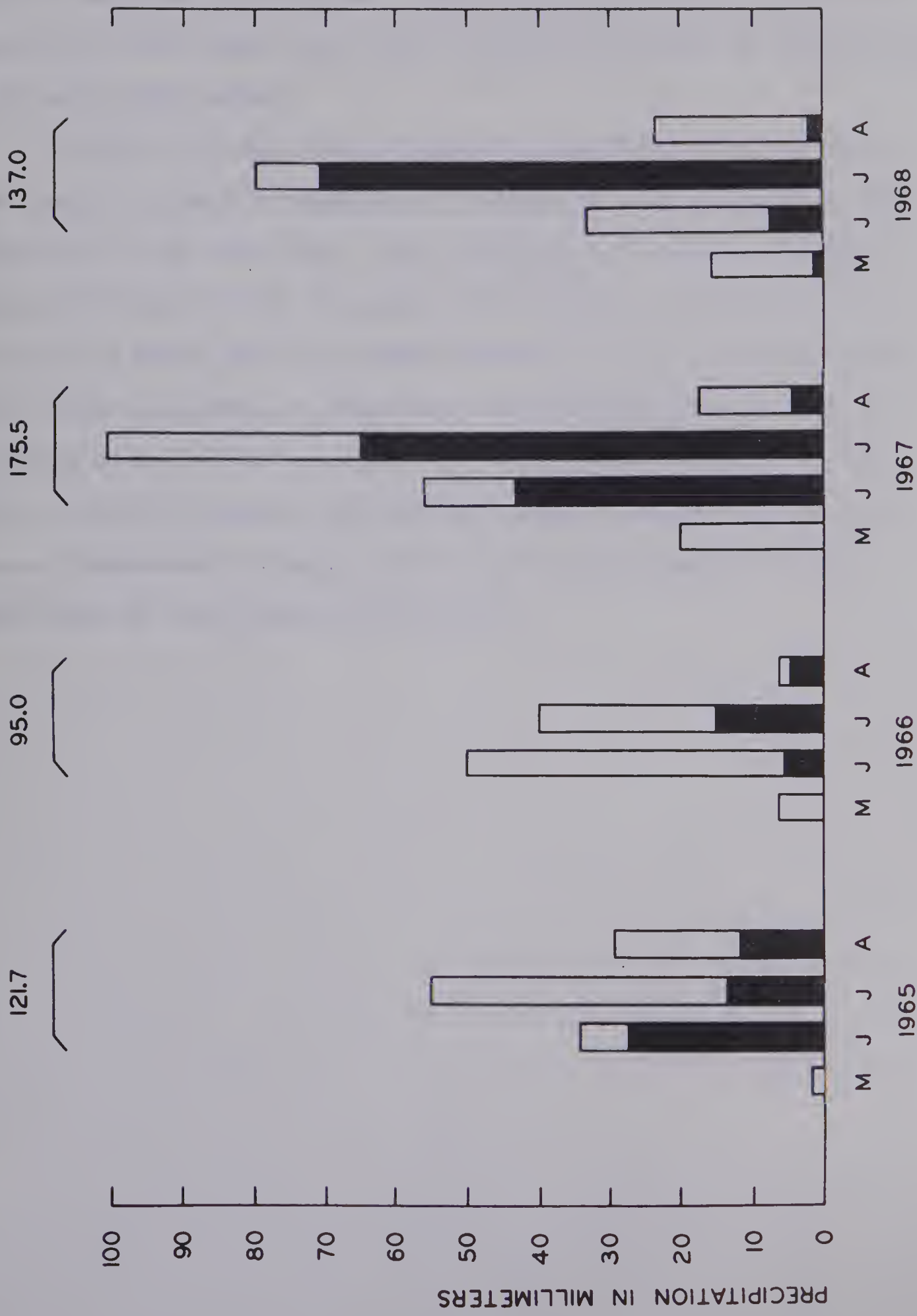








Figure 16. Precipitation in the study area during 1965-1968. The solid part of the bars refers to the first half (1-15) of each month and the open part to the second half. The numbers in the upper part of the figure represent the total precipitation in millimeters for June, July and August. The Hay River normal for this period (Climatology Division, 1965) is 103.1 mm.





time was much higher in 1966 than in 1965, although the opposite was true for the remainder of the summer. Snow had gone by mid-May in the first two years of the study, but in 1967 and 1968 ten and four cm, respectively, fell during that period.

The advent and magnitude of various seasonal aspects of the flora are largely dictated by temperature, rainfall and time of prevernal disappearance of the snow cover. From a phenological standpoint, weather during the four years may be summarized as follows: *at the beginning of the growing season* 1967 was coldest and wettest of the four years and had the longest persistence of snow cover, while 1968 was next in order of severity of these factors and 1966 was wetter and slightly warmer than 1965; *during the flowering and fruiting season* the highest rainfalls and lowest temperatures occurred in 1967 and to a lesser degree in 1968, while 1966 was colder and dryer than 1965.





## METHODS

### Quantitative Habitat Appraisals

The vegetation of each of the 11 associations was quantitatively analyzed in early August of 1968 to determine food and cover potential. Preliminary investigations and examinations of "species: plot number" and "species: area" curves (Vestal, 1949; Oosting, 1958) suggested the suitability of 10 randomly-placed 1-millacre plots, and quarters of these, for determining floral composition. Repetition of the procedure demonstrated its effectiveness for this purpose as well as for estimation of other parameters of the vegetation. A literature review revealed that most sampling techniques for taiga vegetation are based on counts made from transect intercepts rather than on weight determination.

In each habitat 20 circular 1-millacre plots (two surveys of 10), fixed by randomly-chosen coordinates and described by a piece of string 3.7 feet in length (Mosby, 1963), were surveyed for number of fallen trees and proportion of ground litter and cover. The latter was assessed only from herbs and low shrubs which might serve as shelter or hiding places for small mammals, and was estimated from visual vertical projections of foliage to the substratum. The lower, right-hand quadrat of each plot was completely clipped and the stem number ("area" in the cases of mosses and fruticose lichens; "pieces" in the case of *Peltigera* spp.) of each species determined. Wet weights were taken immediately and, after the samples were air-dried, dry weights were also determined. Estimates of numbers of fruits were based on 10 plots only.

In the above fashion it was possible to characterize each habitat by percentage cover and litter, number of fallen logs intercepted per millacre plot, and number and dry weight of aerial growth per millacre of each available and potential food in the lower strata.



(For each of the tracheophytes the average percentage by weight of stems and leaves was determined in case this separation proved necessary.) The dbh, height and spacing of trees were determined by averaging several visual estimates.

To investigate year-to-year variations in vegetative parts of plants, similar sampling (10 plots) was carried out in the *C. rutilus* area during July of 1965 to 1967 in white spruce and mature black spruce; and during 1966 and 1967 in jackpine-juniper. Each year counts of fruits based on 10 plots were made during the first week of June and, save for a week's delay in 1968, during the first week of August. These estimations were made in all three sites with the exception of jackpine-juniper in 1965. Vegetative sampling was carried out throughout the fall of 1965 in white spruce and mature black spruce; and in early (Nov.) and late (Feb.) winter of 1966-67 in all three sites. These latter samples, taken to study seasonal variation, were stored at the University together with the July samples. These three particular communities were chosen for the annual and seasonal surveys because of their rich cricetid faunas and their high number of plant species, the total of which can be taken to represent the flora of the whole forest (excluding clearings). Samples taken from underneath heavy snow covers were not randomly selected.

Throughout the four summers of the study a herbarium was compiled and phenological occurrences documented. Vegetation and fruit production of the surrounding biotypes were noted.

For the most part the works of Raup (1936), Moss (1959), Budd and Best (1964) and Thieret (1963*b*) were used for plant identification and Moss (1955) and Thieret (1964) for vegetation studies. The common names of species mentioned in this work are given in Appendix I. These are



mainly after Moss (1959).

## Population Studies

A survey of methods for censusing small mammal populations revealed the use of three classic procedures, little altered in the recent literature. These are: (1) indirect methods based on abundance of "sign" (Hayne and Thompson, 1965; Vogl, 1967); (2) direct estimation of numbers through Intensive Removal (Hayne, 1949; Grodziński, Pucek and Ryszkowski, 1966; Ryszkowski, Andrzejewski and Petruszewicz, 1966; Aulak, 1967; Elliott, 1969) and Capture-Mark-Recapture (Stickel, 1946; Gębczyńska, 1966; Krebs, 1966; Andrzejewski, 1967; Birkenholz, 1967; DeLong, 1967; Sheppe, 1967; Fuller, 1969a; Nixon and McClain, 1969); and (3) systematic snap-trapping (Hatfield, 1938; Williams, 1955; Kalela, 1957; Hoffmann, 1958; Buchalczyk, 1964; Goertz, 1964a and 1965; Golley *et al.*, 1965; Sharp, 1965; Terman, 1966; Blus, 1966; Iverson, Seabloom and Hnatiuk, 1967) which may have some degree of randomness (Whitaker, 1966, 1967a and b, and 1968).

The last method, which makes use of numerous patterns of trap positions, resembles the first in that it has no value as a measure of absolute density. Its popularity is due to its simplicity and the advantage of obtaining dead animals as a by-product of the census.

For the current study a systematic snap-trapping procedure permitted the use of coefficients of trapping success as relative annual, seasonal and biotopic density indices for the three rodent species. Museum Special snap-traps, baited with peanut butter, rolled oats and bacon grease, a mixture readily distinguishable in the stomach contents, were set 25 feet apart in four lines of 10 stations. Each trap was placed in a favorable position within a 5-foot radius of the station. The number







of individuals of each species taken in this 40-trap grid in one night served as a single value for analysis of relative density. Thus, for statistical purposes, the whole grid was the sampling unit, and not the individual traps.

Traps were relocated after one night to minimize the probability of causing a downward bias in future indices for the given habitat. For the same reason, and to allow time for compensatory recruitment, no biotope (save the large white spruce community of the *C. rutilus* area) was sampled more often than once every three weeks. The local positions of the grids varied randomly with each rota.

Although this method of assessing numbers is judged to have the sensitivity and comprehension urged by Linn (1963), as in all censusing procedures differential trappability is a problem (Gębczyńska, 1966) and results properly apply only to trap-prone individuals whose habits are not typical (Andrzejewski, Petruszewicz and Waszkiewicz-Gliwicz, 1967). The influence of weather, which may (Kalela, 1957; Gentry, Golley and McGinnis, 1966) or may not (Getz, 1968a) be significant, was considered a part of experimental error.

In the summer of 1965 mixed forests and habitats with the richest cricetid faunas were trapped. All 11 study communities were sampled at equal intensity during the summers of 1966, 1967 and 1968 as well as during the winter of 1966-67.

Captured animals were measured, weighed and autopsied, and the data recorded on duplicate punch cards, one set of which is on file at the University of Alberta. Skulls were taken for age determination in other studies. Stomachs for content analysis were removed and preserved in vials of six per cent formalin.



## Food Consumption

Analysis of stomach contents allows the determination of what is actually consumed in nature, but not necessarily what is preferred or nutritionally valuable; nor is it a direct index of availability. Volumetric analyses are valuable for determining the proportional make-up of stomach contents, or for comparing consumption in different times, places, or species. They do not, however, directly indicate rates of consumption since they represent only one feeding period or a portion.

For the present study, contents of preserved stomachs were later examined in the laboratory and the absolute and percentage volumes of their constituents determined. Preliminary studies established that the animals are euryphagous. Therefore, the microtechnical procedures of Baumgartner and Martin (1939), Dusi (1949), O. Williams (1962) and O.B. Williams (*pers. comm.*), which are based mainly on diagnostic clues offered by stained epidermal fragments of leaves, would only be practical during periods when leaf material is eaten in significant amounts. Microtechniques, used to date in analyzing stomach contents and feces of squirrels (Baumgartner and Martin, 1939), rabbits (Dusi, 1949 and 1952; Hayden, 1966), pocket gophers (Keith, Hansen and Ward, 1959; Ward, 1960; Ward and Keith, 1962; Myers and Vaughan, 1965; Vaughan, 1967), *Microtus* (Sharp, 1965), lemmings (Stoddart, 1966) and African grazing herbivores (Stewart, 1967) are not as reliable for estimating volumes of constituents as are the gross distinctions used by European workers (Koshkina, 1957; Shtiľmark, 1965; Droždž, 1966; Holišová, 1966; Fairley, 1967) for animals which depend less on leafy materials.

Pilot examinations also showed that color and consistency were still reliable guides to general categorization even after as long as four years of preservation. Williams (1959), though, found identification more



difficult in preserved stomachs than fresh ones. I agree with Hamilton (1941) that voles chew food items more finely than mice do.

Stomach contents were removed and, in cases where components were naturally segregated, estimates were made immediately. The contents were usually washed in a petri dish of warm water to separate the particles, spread out, and the percentage volume of the constituents estimated to the nearest 10 per cent. Absolute volumes to the nearest 0.1 ml were then determined by volume displacement in a tiny graduated cylinder. Identification was made under a binocular microscope at magnifications up to 35 diameters and frequency of occurrence of all items recorded.

Reference collections from the study area and from known stomach contents allowed identification of the various fruits and lichens, and when fragments were large enough to show venation patterns, of chlorophyllous parts. Figure 17 shows some important cases where *form* was diagnostic. Woody tissue and mushrooms were not identifiable as to kind. I observed in the laboratory that voles extracted the embryo and endosperm of large seeds (e.g. *Rosa woodsii*) and seldom swallowed fragments of the seed coat. These seed contents were not identifiable in the stomach, and thus were added to the "unidentified" category. Occasionally whole fruits with distinctive flesh were consumed (e.g. the unique color of *Geocaulon lividum* berries). Verbal descriptions of diagnostic clues used for the various identifications are listed in Appendix II.

In all, the stomachs of 709 *P. maniculatus*, 238 *C. rutilus* and 292 *C. gapperi* were analyzed (Tables 2 and 3). Other stomachs, obtained from animals of mixed forests by colleagues, were analyzed for annual comparisons, but could not be used for biotopic studies.









Figure 17. Some diagnostically valuable and frequently found entities among the stomach contents of cricetids. All are drawn to the same scale. a-h, seeds; a, *Rubus strigosus*; b, *Fragaria virginiana*; c, *Vaccinium vitis-idaea*; d, *Rubus oxyacanthoides*; e, *R. chamaemorus*; f, *R. acaulis*; g, *Arctostaphylos rubra*; h, *Cornus canadensis*; i, persistent style of *F. virginiana*; j, persistent style of *R. strigosus*; k, ectocarp of *Shepherdia canadensis*; l, "flesh" of *Arcostaphylos uva-ursi* fruit; m, "leaf" of *Hylocomium splendens*; n, *Usnea* spp.; o, *Alectoria jubata*; p - u, leaves; p, *A. uva-ursi*; q, *Populus tremuloides*; r, *Geocaulon lividum*; s, *Linnaea borealis*; t, *Empetrum nigrum*; u, *F. virginiana*; v, arthropod parts.

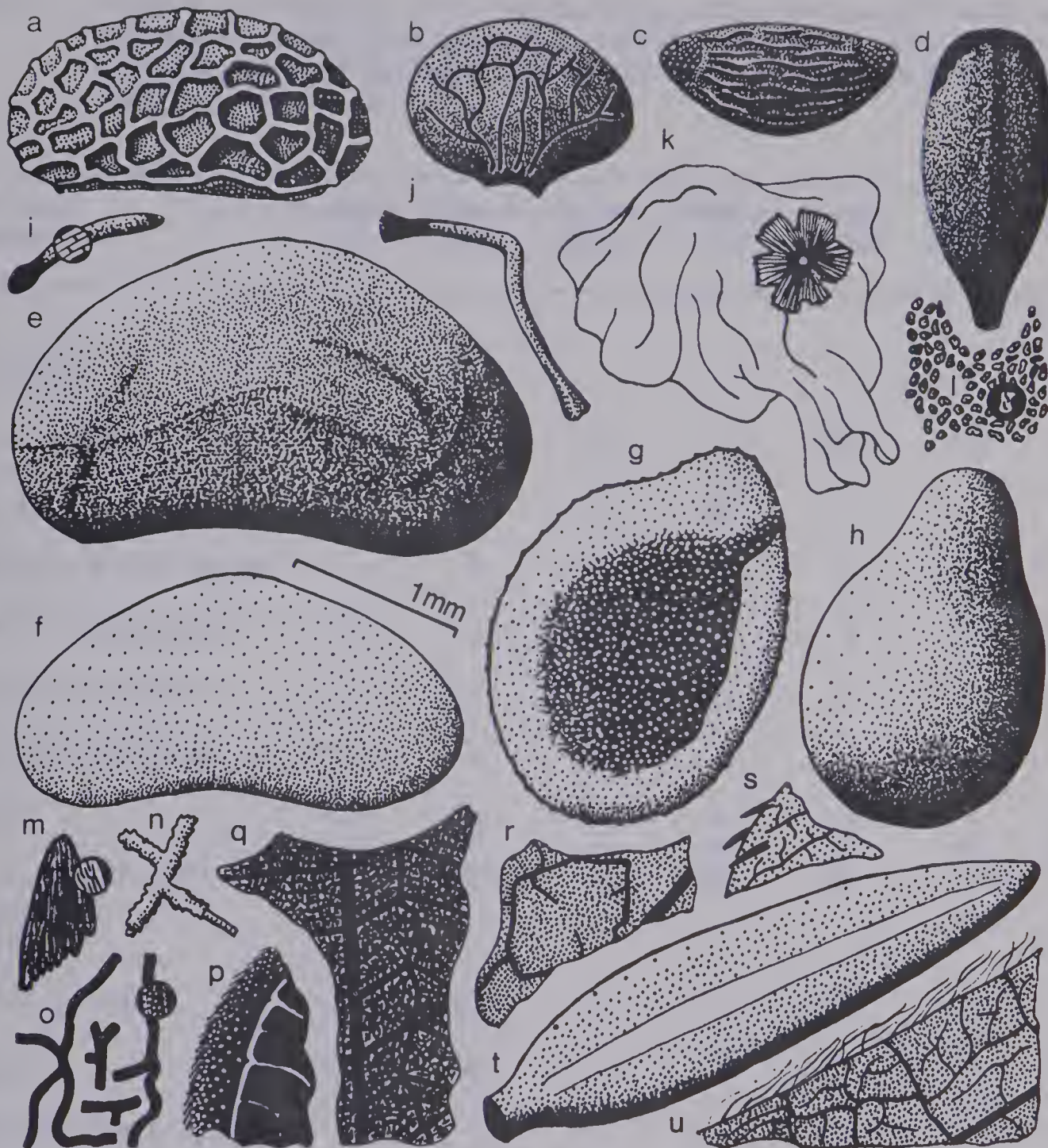






Table 2. Number of stomachs of *P. maniculatus*, the contents of which were examined, classified according to time and area. The summer trapping period includes the second week of May and the first week of September.

Area and biotope	Summer 1965	Summer 1966	Winter 1966-7	Summer 1967	Summer 1968	Winter 1968-9	Total
<i>C. rutilus</i> territory							
White spruce	45	19	2	7	15	1	89
Poplar	--	16	2	10	2	--	30
Immature black spruce	--	2	--	2	--	--	4
Mature black spruce	20	9	4	3	2	--	38
Jackpine-juniper	--	14	4	15	1	--	34
Parklike jackpine	--	1	3	6	1	--	11
Other	99	55	--	--	9	2	165
Subtotal	164	116	15	43	30	3	371
<i>C. gapperi</i> territory							
White spruce	--	10	--	2	--	--	12
Poplar	--	4	--	7	2	--	13
Immature black spruce	--	--	--	--	--	--	--
Jackpine-juniper	8	30	1	12	16	--	67
Parklike jackpine	--	2	--	3	--	--	5
Other	21	148	1	30	26	15	241
Subtotal	29	194	2	54	44	15	338
Total	193	310	17	97	74	18	709





Table 3. Number of stomachs of *Clethrionomys*, the contents of which were examined, classified according to time and area. The summer trapping period includes the second week of May and the first week of September.

Area and biotope	Summer 1965	Winter 1965-6	Summer 1966	Winter 1966-7	Summer 1967	Summer 1968	Winter 1968-9	Total
<i>C. rutilus</i> territory								
White spruce	19	36	12	11	8	8	--	94
Poplar	--	--	--	--	5	--	--	5
Immature black spruce	--	--	4	1	4	--	--	9
Mature black spruce	13	--	6	12	18	--	--	49
Jackpine-juniper	--	--	--	1	3	--	--	4
Parklike jackpine	--	--	1	--	6	--	--	7
Other	<u>28</u>	<u>12</u>	<u>21</u>	<u>--</u>	<u>--</u>	<u>5</u>	<u>4</u>	<u>70</u>
Subtotal	60	48	44	25	44	13	4	238
<i>C. gapperi</i> territory								
White spruce	--	--	12	6	3	--	--	21
Poplar	--	--	4	9	17	3	7	30
Immature black spruce	--	--	3	--	5	--	--	8
Jackpine-juniper	11	14	16	4	9	5	--	59
Parklike jackpine	--	--	--	--	--	--	--	--
Other	<u>7</u>	<u>18</u>	<u>110</u>	<u>3</u>	<u>17</u>	<u>14</u>	<u>5</u>	<u>174</u>
Subtotal	18	32	145	22	41	22	12	292
Total	78	80	189	47	85	35	16	530



## Food Preference

Consumption has often been equated with food preference although most investigators acknowledge the importance of availability, accessibility and palatability. The ratio of consumption to availability as an index of selection has been used particularly in recent studies of pocket gophers (Ward and Keith, 1962; Myers and Vaughan, 1965; Vaughan, 1967), sparrows (West, 1967) and, with slight methodological variations, lemmings (Stoddart, 1966), *Clethrionomys glareolus* (Holišová, 1966), grouse (Phillips, 1967) and mountain goats (Hibbs, 1967). The disadvantages of this quotient as a measure of preference lie in the arbitrary decisions of what foods are accessible, and in the need for a prior knowledge of consumption.

Preferences determined through experimentation are subject to the shortcomings of the laboratory approach to natural history, and can be misleading if regarded as more than an indication of the natural situation. These methods may be: (1) watching the animals (Horner, Taylor and Padykula, 1965; Samuel, 1967) or observing the state of the remains of foods offered (Cogshall, 1928; Menhusen, 1963; Thompson, 1965); (2) "cafeteria" tests similar to those of Arnold (1942), Radwan and Campbell (1967) and Samuel (1967). The former method lacks quantitative expression, and the latter relies on ranking methods, an example of which is the popular "4-point" or "4-grade" scale of food preference (Miller, 1954; Sviridenko, 1961; Górecki and Gębzyńska, 1962; Petrov, 1963; Drożdż, 1966 and 1967; see also Beck, 1952).

There is obviously a need for a preference apparatus and procedure which does not produce a few grades of preference, but which employs a continuous scale, permitting statistical comparisons of the values for



various foods and an appreciation of *degree* as well as *kind* of preference differences. That described below attempts to fulfill this requirement.

Several "T-mazes" measuring 20 X 16 X 5 inches were constructed of hardware cloth and wooden ribbing on plywood bottoms (Fig. 18). From the corridor or the detachable cage, a subject had full visibility of each of the food compartments, which could be reached only through a swinging door which activated a switch. These units had the physical advantage of being sturdy, "leakproof" and, since the compartments and switches were accessible to the worker through a single cover, convenient.

For each preference test an adult subject was offered a choice between the food to be tested in one compartment and Labena laboratory food (a control of known and constant composition which does not crumble) in the other (Fig. 19). The *number of passages* to and from each chamber and the *time spent* was read from the chart paper (Fig. 20) of an Esterline-Angus event recorder (Figs. 18 and 19), and the *amount of food eaten* was determined by weighing. Thus, three indices of preference were constructed according to the formulae of Figure 20.

For the *weight* index, an equal amount of natural food was placed outside the chamber to correct for water loss through evaporation. Berries were crushed so that the exposed surfaces of the evaporation controls would more closely resemble those of the chewed foods in the compartments. No evaporation control was necessary for the dry laboratory pellets. Natural foods were supplemented at intervals to mollify the effects of drying on palatability; and a supply of fresh water was always available.

Pilot studies indicated, via the signal patterns (Fig. 20), that the animals spent little time out of their nestboxes. This appears to be characteristic of wild-caught rodents. Also, they seldom entered the







Figure 18. Laboratory set-up showing an event recorder and several food-preference units.

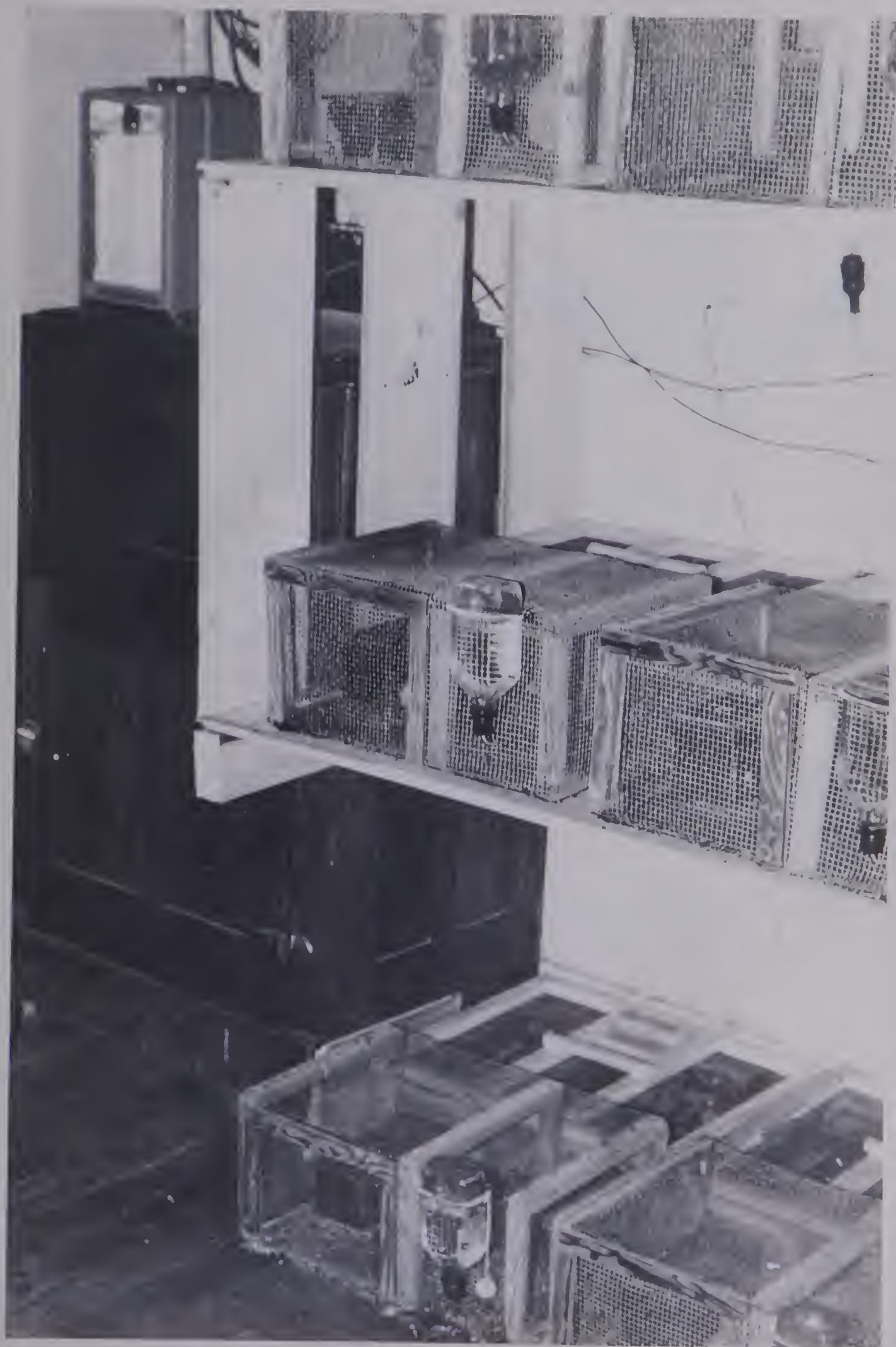






Figure 19. A semi-schematic representation of a single 2-choice maze with attached cage connected to an Esterline-Angus event recorder. An enlarged mercury switch is depicted at upper right. a, detachable cage; b, nestbox; c, water bottle; d, compartment entrance containing swinging door; e, mercury switch housing; f, food tray; g, wires connecting switches to electromagnets of event recorder; h, event recorder; i, clock-operated chart; j, swinging door; k, mercury; l, plexiglass tubing; m, tungsten electrodes. In reality, the maze was not solid.



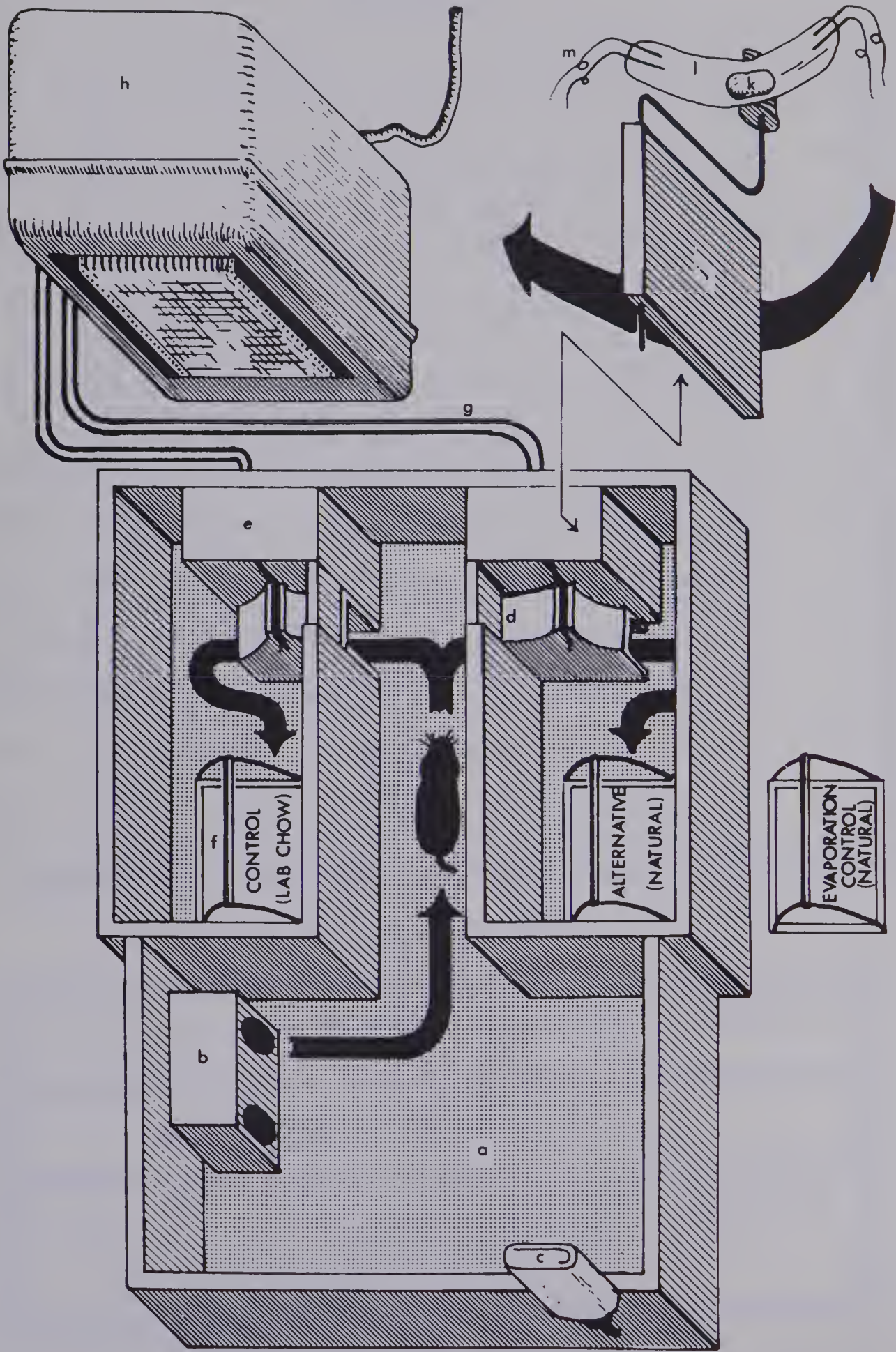
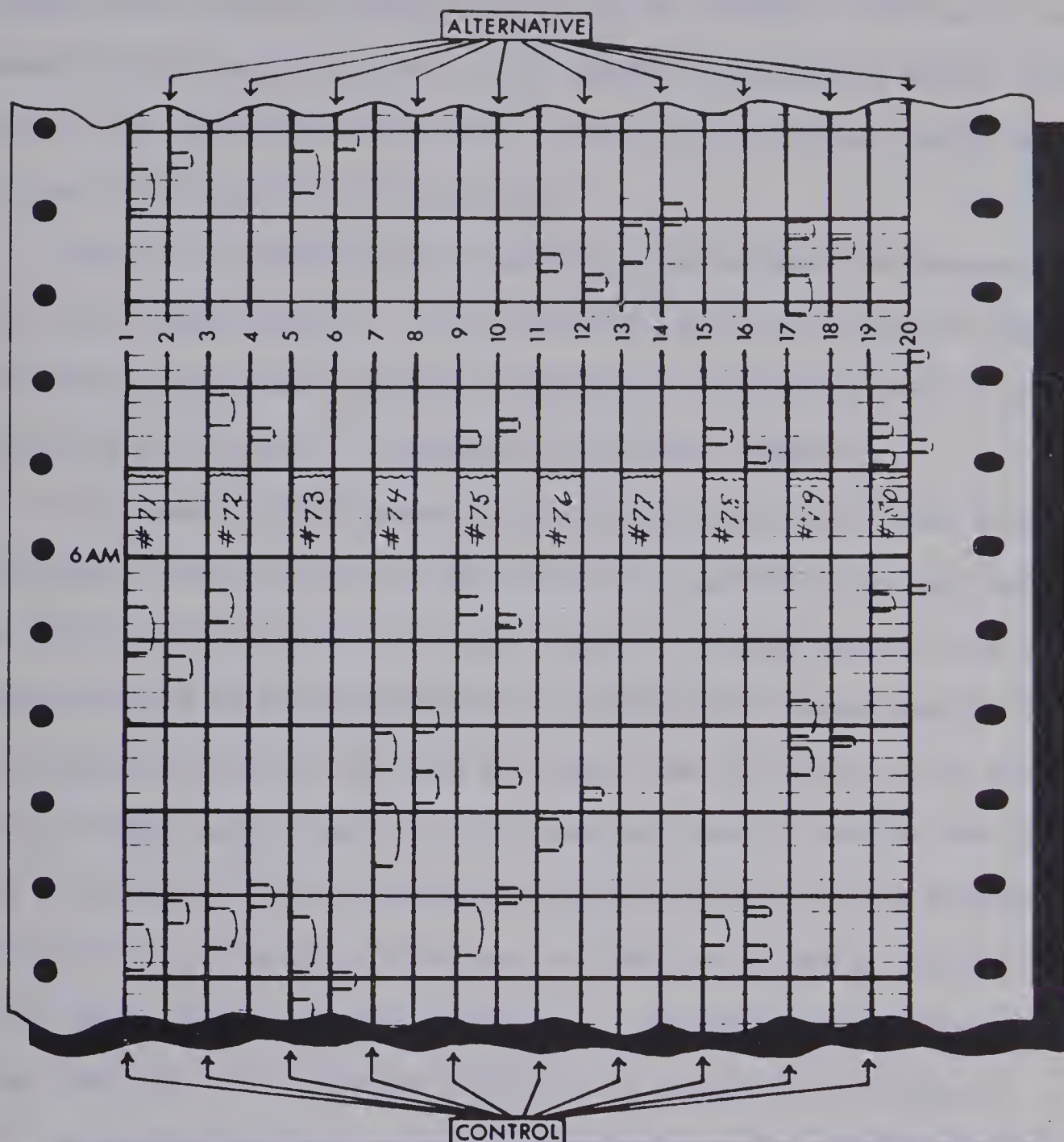






Figure 20. A section of chart roll from an Esterline-Angus recorder showing the number of passages and the time spent in each chamber for ten tests executed concurrently. Below are shown the formulae for the three food preference indices. Note that visitations are contiguous and of short duration.





$$\text{"PASSAGE" INDEX} = \frac{\text{NO. OF PASSAGES TO AND FROM ALTERNATIVE CHAMBER} \times 100}{\text{TOTAL NO. OF PASSAGES}}$$

$$\text{"TIME" INDEX} = \frac{\text{TIME SPENT IN ALTERNATIVE CHAMBER} \times 100}{\text{TOTAL AMOUNT OF TIME SPENT FEEDING}}$$

$$\begin{aligned} \text{"WEIGHT" INDEX} &= \frac{\text{WT. LOSS OF ALTERNATIVE} - \text{WT. LOSS OF EVAPORATION CONTROL}}{\text{TOTAL WT. OF FOOD CONSUMED} \times 1/100} \\ &= \frac{\text{WT. OF ALTERNATIVE CONSUMED} \times 100}{\text{TOTAL WT. OF FOOD CONSUMED}} \end{aligned}$$





chambers when food was placed in the cage or corridor, and thus it was suspected that the time spent in the chambers represented mostly "foraging" rather than spontaneous behaviour. A correlation between *weight* and *time* indices would bear out this suspicion.

There was no problem with food being removed from the chambers by any of the three species. The switch door, which was heavy and suspended from above, served the secondary functions of preventing such removal and providing an impediment to excessive use of the chambers.

To eliminate any dissymmetry caused by factors other than food preference, the positions of the control and natural foods were switched at the half-way point of each test. Since a 24-hour interval was deleted from the chart at the beginning of each half of the experiment to allow for familiarization of the food positions, and since each trial was carried out for eight days, a period of six days was used to compute the *passage* and *time* indices. New subjects were allowed a few days for adjustment before testing. Deermice were seen to forage nocturnally, whereas the voles exhibited 2-3 hour peregrinations. The use of whole days, rather than fractions, was therefore necessary to compare the two genera.

Because of the wide range of variation caused by individual preference, and the influence of experimental error, several values for the same food were necessary to obtain a representative mean. The number of replicates for each of the 30 foods bioassayed varied between 4 and 15, representing a total of over 600 tests. Some *weight* tests were run without recording *time* and *passage* indices because of limitations on the number of recorder terminals available. Discrepancies between the sample number of the *time* and *passage* indices occurred whenever there was a delay in fixing a switch that was firing in one direction only.



The choice of foods to be tested was partly subjective. Decisions were based on (1) results of consumption studies, (2) the prevalence of a food in the study area and (3) the value of the food as a representative of a "type" (e.g. woody stems, succulent fruits). To approximate the natural situation, animals and food were collected immediately prior to the experiment and kept no longer than three months. During the winter of 1966-67 it was possible to test a limited number of foods on *P. maniculatus* and *C. gapperi* which were live-trapped in small numbers. This work was done at the Heart Lake Laboratory as were the studies in early summer, 1967. Experiments in early summer, 1968, and during the fruiting seasons of 1967 and 1968 were done at the university. Most tests were done during the fruiting season when the variety of foods was greatest and subjects most easily captured.

Throughout the trials temperature was maintained within a few degrees of 20° C and subjects were exposed to natural photoperiod. At the university the only light source was a small window, so intensity was lower than normal during daylight hours. To take maximum advantage of this light the mazes were not separated (Fig. 18) and, consequently, it was possible for an animal in a compartment of one unit to see, smell and hear his neighbor. Thus social facilitation could have occurred. To test for this the number of coincident visits to adjacent chambers was compared with the number to be expected by chance and no significant differences were found. Nevertheless, experiments of this sort (especially if different animals are used) probably ought to be carried out with food-preference units in visual, auditory and olfactory isolation to minimize the influences of social facilitation, physical attraction, displacement, or avoidance on the independent operation of the subjects. Thompson (1965) was forced to



separate units containing *Microtus pennsylvanicus* which were visually isolated, because they detected one another's presence by other means and tried to gnaw through walls separating them from their neighbors.

In the course of a test period a progressive decrease in preference for a given food was detectable in the majority of subjects according to the *time* and *weight* indices. This downward trend, which may be attributed to satiation or loss of novelty, was very slight. It was apparently greatest in *P. maniculatus* and least in *C. gapperi*.

The possibility of using more than one animal simultaneously was ruled out because of the staggering complex of social behavioural variables involved, and because it would not be possible to read the time spent in each food compartment if several animals were operating at the same time. This idea would have some merit if the *passage* index alone were used.

Since this is a new method of determining food preference, additional explanations are in order:

1. A *control* food was used instead of a comparison of two natural foods:
  - a) to prevent death or suffering of test animals when natural foods of inadequate nutritional value were offered; and
  - b) so that preference could be rated on a continuous scale and the results treated statistically.
2. A *two-chambered situation* was used instead of a multi-choice apparatus because:
  - a) with only one food tested at a time there were no interactions caused by the presence of other foods;
  - b) only a single change-over was required to eliminate dissymmetry





as opposed to the complicated regimen required in the more elaborate apparatus; and

- c) lab food in a multi-chambered unit would have to be equidistant from each of the natural foods, which would probably decrease the number and length of visitations to the latter, and thus the significance of the data.

Unlike most methods, where very few subjects and/or trials are used, the present procedure involved a great amount of work both in manipulating foods and in reading the chart paper because of the repetitions required. This was its major drawback.

### Maintenance Values

Maintenance values of various natural plant foods of the three rodent species were determined in the laboratory by presenting these foods, *ad libitum*, singly, and in combination, to individual adult, non-breeding animals that had previously maintained constant weight on Labena pellets. They were housed singly and provided with a constant supply of fresh water. Other conditions were identical to those described for the preference tests.

Indicators of maintenance "value" of a given food were (1) rate of weight loss or gain and (2) time until death. Similar studies have been reported by Koshkina (1957), Samuel (1967), Tietjen *et al.* (1967) and Bailey (1969). Choice of foods for these bioassays was based on foods found in stomachs and the results of preference tests.

### Rates of Water and Lab Chow Consumption

To compare requirements of the three species, water and Labena consumption rates were determined in the laboratory for some of the animals.



A narrow range of temperature ( $20^{\circ}\text{C} \pm 5$ ) and natural photoperiod were maintained, and the animals (non-reproductive adults) were housed individually in cages similar in size to those used in the other experiments. Measurements were taken only after the animals were established under these conditions for at least a month. Water was presented in graduated bottles, and since the diet consisted of Labena pellets, no other water source was available. Water and food consumption were recorded for periods of more than 25 days.

### Statistical Procedures

Although many statistical works were consulted for analysis of data, those of Moroney (1951), Simpson, Roe and Lewontin (1960) and Ostle (1963) were most used. Tests of significance employed Yates' and Bessel's Corrections for  $\chi^2$ - and  $t$ -distributions, respectively. Specific procedures are described in the appropriate section of RESULTS.





## RESULTS

### Habitat Appraisals

Phenology. As compared to more southerly areas, the phenology of the growing season on the study area was compressed as a result of its swift progression; and, in spite of some "telescoping" of events (Raup, 1935), its general aspects appeared compartmentalized.

Green leaves and shoots appeared suddenly in late May and reached full development within the first two weeks of June. Among the first were those of *Pyrola asarifolia*, *Ribes oxycanthoides*, *Geocaulon lividum*, *Cornus canadensis* and *Populus tremuloides*. *Shepherdia canadensis*, *Rosa woodsii* and *Viburnum edule* were the last to leaf.

The flowering season lasted from the last week in May (*Shepherdia canadensis*, *Arctostaphylos uva-ursi*, *A. rubra*, *Empetrum nigrum*, *Ribes oxycanthoides*) to the first week of July (*Linnaea borealis*, *Moneses uniflora*, *Epilobium angustifolium*), with a peak in mid-June (*Rubus strigosus*, *Geocaulon lividum*, *Viburnum edule*, *Vaccinium vitis-idaea*, *Rosa woodsii*, *Cornus canadensis*).

Fruits ripened mainly in the last week of July although some matured in early July (*Shepherdia canadensis*, *Fragaria virginiana*, *Ledum groenlandicum*, *Juniperus* spp.) and others as late as mid-August (*Cornus* spp.).

After mid-August frosts were frequent. The first snow fell in early October when the ephemeral fruits (those which do not overwinter on the plant) had almost all disappeared, and all leaves save those of the evergreens were dying. The snow cover lasted until early May.

Six fruits overwintered and some of their diminishing numbers lasted until new ones of the same species ripened. Of these, *Vaccinium oxycoccus*



and *Arctostaphylos rubra* were scarce, whereas the berries of *Juniperus* spp., *Rosa woodsii*, *V. vitis-idaea* and *A. uva-ursi* overwintered in relative abundance. These, along with the vegetative parts of overwintering plants, lichens and a few overwintering insects, were potential food sources during the 7- to 8-month winter.

Mushrooms (mainly *Russula* sp. and *Hydnellum* sp.) were found only during the growing season (as early as the latter part of May) and were most abundant in the first week of August. Arthropods were present mainly during the summer months.

The beginnings of several phenological occurrences are given in Appendix III for 26 tracheophytes arranged in order of importance as food and as conspicuous indicators of the favorableness of the season. These values, taken from my field journals, are of exaggerated accuracy since they represent a period rather than a point in time. Dates were recorded upon first sighting the event (i.e. spreading of leaves, inflorescence in full bloom). When this was not possible, estimates were based on related observations.

The summers of 1967 and 1968 were characterized by phenological lags which were never made good. Yearly comparisons of the flowering and fruiting times in the nine most important food plants (Fig. 21) exemplify this delay which was of one to two weeks' duration depending on the species. The mean delay over 1966 was 11 days for flowering time and 12 for fruiting in the nine species shown. The rough nature of the data dissuades the drawing of any firm conclusions regarding interspecific differences, although the plants which bore overwintering fruits, important in the present study, appeared to have been particularly subject to delay.

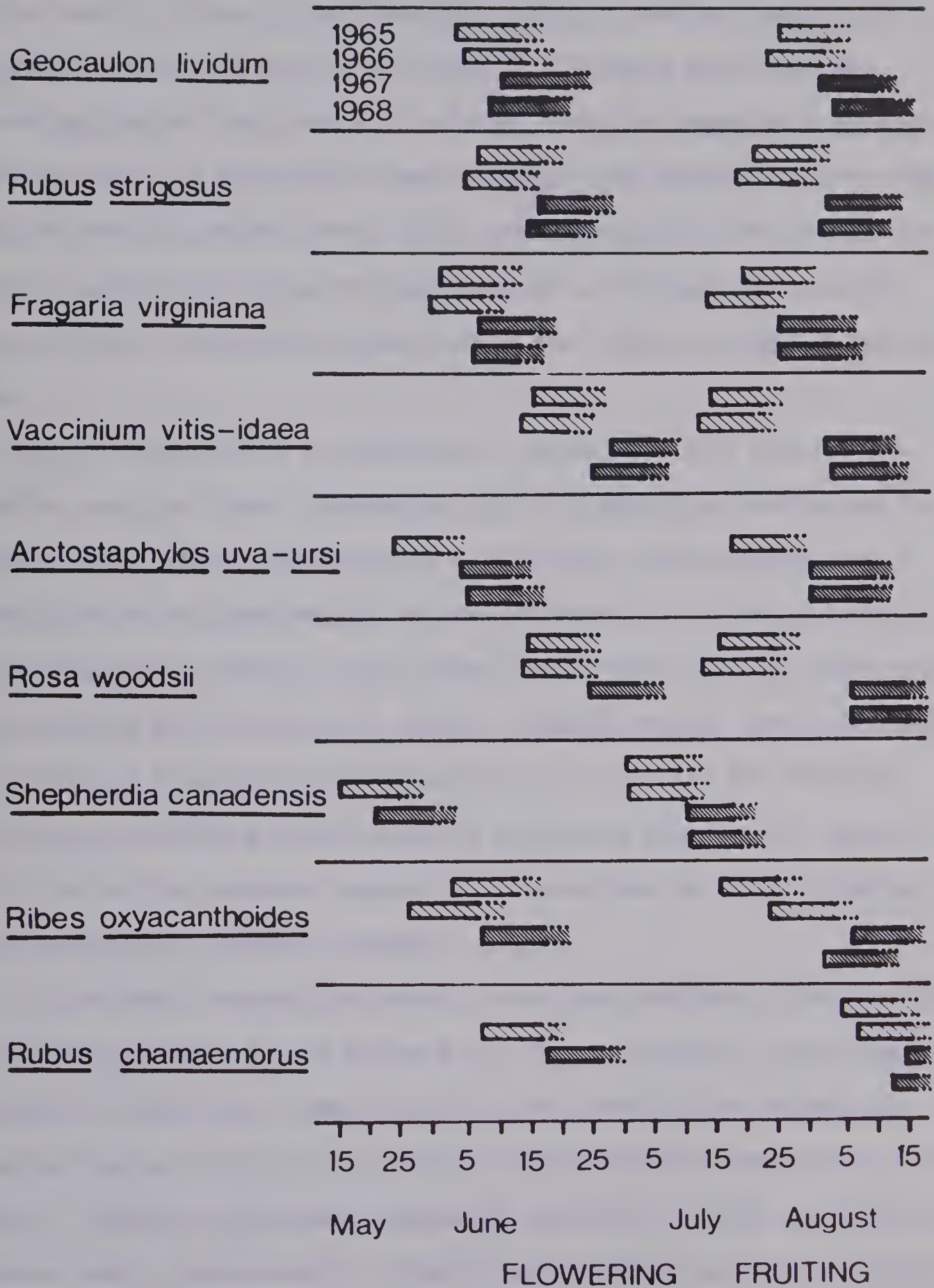
Earlier phenological dates were recorded for 1966 than for 1965 in





Figure 21. The appearance of flowers and fruits in nine plant species of dietary importance for the present study. The late years are differently cross-hatched for emphasis.







25 out of the 31 cases where the data allowed comparisons (two cases gave similar dates). These differences were slighter than the lags of 1967 and 1968 and, for the species of Figure 21, averaged seven days for flowering time but only four for fruiting. Similar comparisons between 1967 and 1968 were difficult to make because I was absent from the study area for certain periods during those years (especially 1968) and, consequently, many of the dates are approximations. Although the data are not conclusive, the overall impression is that 1967 was slightly behind 1968.

Spatial differences in phenological advent were also noted. Considering only the floral composition, the 11 communities studied may be grouped into: white spruce-poplar; black spruce; and jackpine. An examination of the phenological records of Appendix III, in conjunction with Appendix IV, indicates that plants characteristic of the white spruce-poplar forest are the latest to flower, although they do not appear to be any different from the others in their times of leafing and fruiting. The flora of the black spruce shows no particular phenological pattern while that of the jackpine forests is characterized by early flowering and fruiting (and probably leafing).

Of the more cosmopolitan plants, *Ledum groenlandicum* bloomed earlier in the immature than in the mature black spruce in 1966. In the same year *Geocaulon lividum* first came into flower and fruit in the muskegs and jackpine-juniper forests, and *Linnaea borealis* fruited more quickly in the latter. *Fragaria virginiana*, *Shepherdia canadensis*, *Pyrola asarifolia*, *Viburnum edule*, *Rubus acaulis*, *Mitella nuda*, *Linnaea borealis* and *Cornus canadensis* bloomed first in the more open areas. In 1967, rose bushes were seen to come into leaf earlier in clearings. Indeed, in each spring





the roadsides turned green earlier than the interior of the forests.

Herbarium specimens collected in 1965, 1966 and 1967 were usually taken from open areas where they bloomed before their counterparts in the woods.

Production. Each year's production of above-ground vegetative parts is summarized in Tables 4 and 5 for three biotopes in *C. rutilus* territory. The jackpine-juniper forest was not sampled in 1965 and, since I was not in the field during midsummer of 1968, that year is not represented. Only species which bear fruits of dietary importance are given individual attention since vegetative parts were found not to be important at that time of year.

The sampling method used, which brings out biotopic differences with facility, is not very effective for detecting slight yearly variations in the standing crop. This is especially true for scarce species. Thus, although Table 4 generally suggests a peak standing crop in 1966 with a drop in 1967, only the 1966-67 decrease in *F. virginiana* of the jackpine-juniper plot was statistically significant ( $p < 0.05$ ).

Narrower and more workable variance is obtained, however, when the weights of individuals are compared. Table 5 gives a general impression of a 1966 peak in biomass at the individual level, with a decrease the following summer. The 1965-66 increase was significant at the five per cent level in white spruce for *G. lividum* and for the collective shrubbery excepting *S. canadensis* and *R. woodsii*. In mature black spruce the increase was significant in *V. vitis-idaea* and *G. lividum*. Significant drops in 1967 are seen in the white spruce forest for *G. lividum* and for *R. woodsii* which also dropped from 1965. In the jackpine-juniper forest this drop is significant in *G. lividum* and for the remaining collective herbage excepting *F. virginiana*.





Table 4. Mean dry weight per millacre ( $\pm$ S.E.) of aerial biomass in three biotopes of *C. rutilus* territory taken during June 22-July 16, 1965; July 10-15, 1966; and June 28-July 5, 1967. The sample number is 10.

Species		1965 (gm)		1966 (gm)		1967 (gm)	
White spruce	Shrubs:						
	<i>S. canadensis</i>	24.3	$\pm$ 13.2	28.6	$\pm$ 19.9	23.0	$\pm$ 12.7
	<i>R. woodsii</i>	12.9	$\pm$ 4.3	12.8	$\pm$ 4.0	13.8	$\pm$ 5.8
	Others	6.8	$\pm$ 2.3	18.9	$\pm$ 9.3	4.0	$\pm$ 2.1
	Herbs						
	<i>G. lividum</i>	4.7	$\pm$ 3.0	7.1	$\pm$ 2.8	3.4	$\pm$ 2.3
	<i>F. virginiana</i>	0.79	$\pm$ 0.64	0.40	$\pm$ 0.32	0.43	$\pm$ 0.32
	Others	22.7	$\pm$ 5.2	28.6	$\pm$ 4.4	23.5	$\pm$ 8.6
	Ground Cover	1054	$\pm$ 252	962	$\pm$ 310	1066	$\pm$ 206
Mature black spruce	Shrubs:						
	<i>R. woodsii</i>	29.1	$\pm$ 9.2	22.4	$\pm$ 4.8	16.9	$\pm$ 5.8
	<i>V. vitis-idaea</i>	208.4	$\pm$ 44.8	292.1	$\pm$ 63.4	215.0	$\pm$ 49.2
	Others	848.2	$\pm$ 247	652.8	$\pm$ 135	726.5	$\pm$ 197
	Herbs						
	<i>G. lividum</i>	0.80	$\pm$ 0.60	1.65	$\pm$ 0.85	1.36	$\pm$ 0.71
	Others	1.12	$\pm$ 0.83	1.20	$\pm$ 0.93	0.81	$\pm$ 0.62
	Ground Cover	1011	$\pm$ 253	1109	$\pm$ 261	1410	$\pm$ 212
Jackpine-juniper	Shrubs:						
	<i>S. canadensis</i>			32.3	$\pm$ 28.9	20.6	$\pm$ 13.7
	<i>R. woodsii</i>			5.11	$\pm$ 1.44	4.60	$\pm$ 1.39
	<i>A. uva-ursi</i>			178.4	$\pm$ 36.2	184.2	$\pm$ 59.1
	<i>V. vitis-idaea</i>			9.08	$\pm$ 4.94	3.00	$\pm$ 2.41
	Others			35.4	$\pm$ 17.1	36.6	$\pm$ 16.8
	Herbs:						
	<i>G. lividum</i>			2.72	$\pm$ 1.39	0.76	$\pm$ 0.51
	<i>F. virginiana</i>			0.44	$\pm$ 0.23	0.08	$\pm$ 0.08*
	Others			74.8	$\pm$ 19.7	73.8	$\pm$ 25.3
	Ground Cover			2456	$\pm$ 214	2052	$\pm$ 209

\*Significantly different from the previous year ( $p < 0.05$ )



Table 5. Mean dry weight per stem ( $\pm$ S.E.) of aerial biomass in three biotopes of *C. rutilus* territory taken during June 22-July 16, 1965; July 10-15, 1966; and June 28-July 5, 1967. The sample number is shown in parentheses.

Species		1965 (gm)			1966 (gm)			1967 (gm)		
White spruce	Shrubs:									
	<i>S. canadensis</i>	7.62	± 2.24	(5)	9.23	± 7.73	(3)	9.20	± 4.22	(3)
	<i>R. woodsii</i>	1.28	± 0.37	(5)	1.67	± 0.36	(6)	1.30	± 0.47	(7)
	Others	0.95	± 0.29	(8)	1.95	± 0.42	(4)*	1.36	± 0.67	(4)
	Herbs:									
	<i>G. lividum</i>	0.10	± 0.02	(5)	0.21	± 0.38	(6)*	0.12	± 0.010	(2)
	<i>F. virginiana</i>	0.043	± 0.01	(5)	0.051	± 0.02	(2)	0.026	± 0.01	(3)
Others	0.065	± 0.009	(10)	0.076	± 0.009	(10)	0.058	± 0.009	(10)	
Mature black spruce	Shrubs:									
	<i>R. woodsii</i>	2.58	± 0.71	(8)	2.11	± 0.46	(8)	0.76	± 0.23	(8)*†
	<i>V. vitis-idaea</i>	0.098	± 0.020	(10)	0.26	± 0.070	(10)*	0.14	± 0.028	(10)
	Others	3.59	± 0.57	(10)	3.23	± 0.36	(10)	3.41	± 0.61	(10)
	Herbs:									
	<i>G. lividum</i>	0.073	± 0.014	(3)	0.16	± 0.034	(3)*	0.050	± 0.015	(4)*
	Others	0.080	± 0.025	(2)	0.070	± 0.049	(2)	0.080	± 0.026	(3)
Jackpine-juniper	Shrubs:									
	<i>S. canadensis</i>				3.03	± 1.37	(5)	3.41	± 0.18	(4)
	<i>R. woodsii</i>				0.21	± 0.04	(7)	0.24	± 0.06	(9)
	<i>A. uva-ursi</i>				0.65	± 0.06	(10)	0.61	± 0.055	(10)
	<i>V. vitis-idaea</i>				0.17	± 0.029	(3)	0.10	± 0.050	(2)
	Others				2.30	± 0.89	(5)	4.17	± 0.91	(6)
	Herbs:									
<i>G. lividum</i>				0.15	± 0.011	(4)	0.10	± 0.012	(2)*	
<i>F. virginiana</i>				0.18	± 0.11	(3)	0.13	±	(1)	
Others				0.07	± 0.016	(10)	0.12	± 0.013	(10)*	

\*Significantly different from the previous year ( $p < 0.05$ )  
†1967 significantly different from 1965 ( $p < 0.05$ )



Much greater variation was found in fruit production (Fig. 22). That 1966 produced the greatest fruit crops in *G. lividum*, *S. canadensis*, *R. woodsii*, *A. uva-ursi* and *V. vitis-idaea* was obvious even upon casual observation of the plots. (In addition, fruits of *Rubus strigosus* in open areas and those of *Ribes oxycanthoides*, *Viburnum edule* and *Rubus acaulis* which ripened later than the time of the surveys of Figure 22, were most plentiful in 1966.) The 1966-67 decline in production was significant ( $p < 0.05$ ) in the white spruce forest in *G. lividum*, *R. woodsii* and *A. uva-ursi*; in the black spruce stand in *G. lividum*, *R. woodsii*, and *V. vitis-idaea*; and in the jackpine in *G. lividum*, *F. virginiana*, *R. woodsii*, and *V. vitis-idaea* (Fig. 22).

Although the 1965 fruit crop may have been generally inferior to that of 1966, and no differences could be detected between 1967 and 1968, *F. virginiana* showed a significant increase ( $p < 0.05$ ) in fruit numbers in 1968 to produce a higher crop than that of 1965, the second highest year (Fig. 22). Verges fronting the white spruce and poplar communities of *C. rutilus* territory produced especially great numbers of these fruits in 1965 and 1968.

In the case of fruits which overwinter on the plants, availability has an extended importance. Densities in June were highest in 1967 following the peak production of 1966, and almost reached zero in 1968 following the poor season of 1967. Such changes in numbers were significant at the five per cent level in all cases except that of *V. vitis-idaea* following the crops of 1965 and 1966.

No "seed years" (Koshkina, 1957; Lauckhart, 1957) were observed during the four years, insofar as the term applies to tree seeds. Individual mushrooms had to be actively sought out during the first two summers





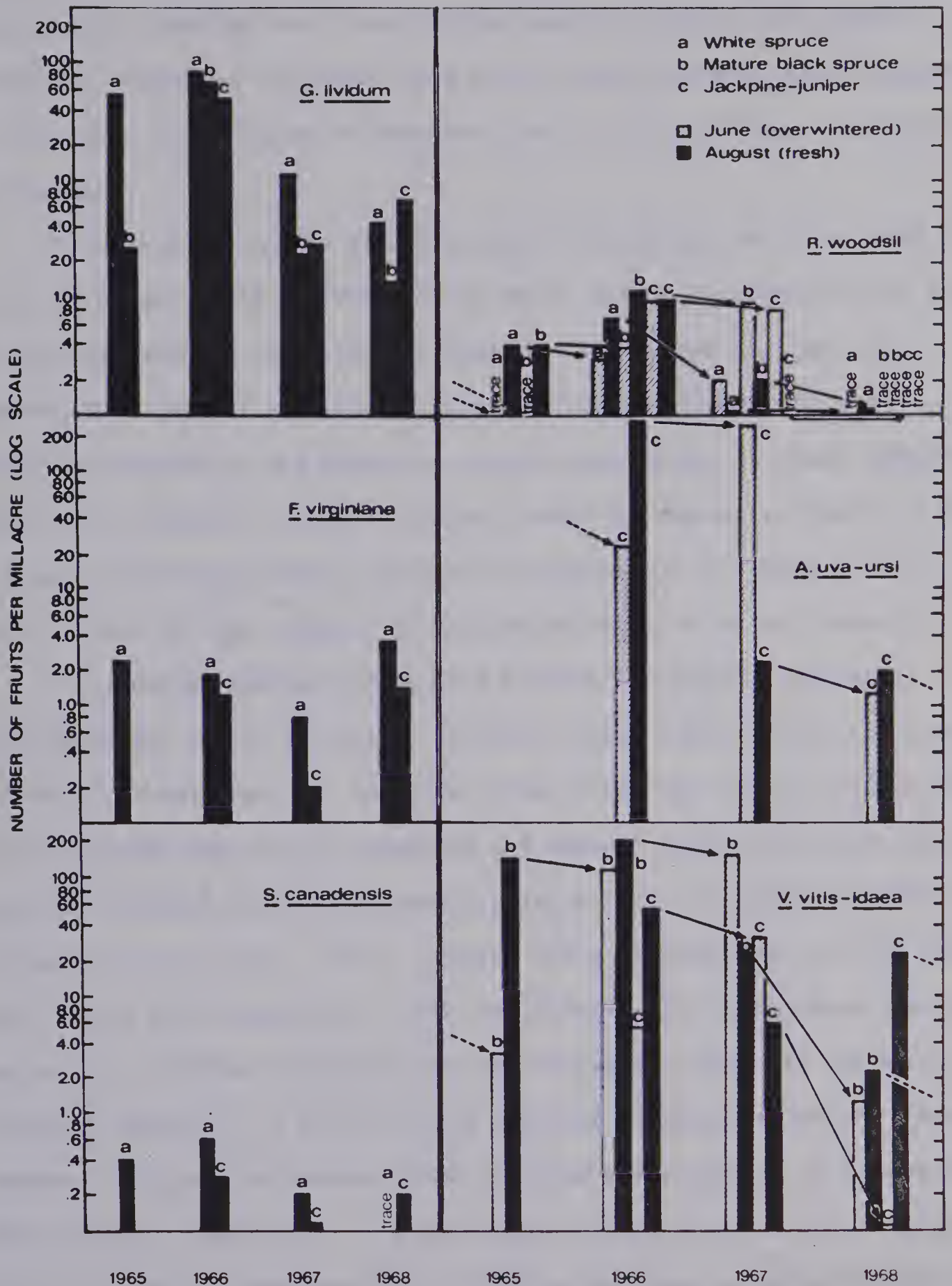




Figure 22. Mean number of fruits per millacre for six important species in three biotopes of *C. rutilus* territory during 1965-68. Arrows connect fresh fruits in August to their overwintered densities the following June. All means are based on 10 estimates.

EPHEMERAL FRUITS

OVERWINTERING FRUITS





of the study, although perhaps with greater ease in 1966. In 1967 these (especially *Hydnellum* and, later in the season, *Russula*) were found in abundance throughout the study area when I noted that they also abounded in the Peace River region of northern Alberta. In 1968 they were almost as abundant.

Biotope measurements of production, taken during the first week of June and August, 1968 to determine seasonal changes in biomass, were found to show differences even slighter than the annual ones and, for that reason, both sets of measurements are combined in Appendix IV to show spatial variation in the floristic compositions of the 11 plant communities. None of the habitats showed an obvious dearth of vegetative foods, so only the important fruit bearing species are singled out in Tables 6 and 7, whose values are now examined by biotope beginning with the richest.

The jackpine-juniper stands were highest in overall production, especially the one in *C. rutilus* territory which contained all the species listed in Tables 6 and 7. In spite of the relatively low *G. lividum* biomass in this particular plot it contained the highest numbers of fruits of this species, although only significantly greater ( $p < 0.05$ ) than the densities of mature black spruce. The *C. gapperi* stand produced none of this species. Both stands held heavier ( $p < 0.01$ ) individuals of *F. virginiana* than white spruce of *C. rutilus* territory, the only other site where it was plentiful enough to measure. In spite of this apparent superior productive potential, however, the jackpine-juniper plots retained fewer berries of *F. virginiana* than the less open areas. *V. vitis-idaea* was not found in the *C. gapperi* stand, and in its complement of *C. rutilus* territory produced significantly fewer berries ( $p < 0.05$ ) than in the other sites where it occurred. *A. uva-ursi*, on the other hand, was rivalled in production only by the parklike





Table 6. Production (mean  $\pm$  S.E.) of important plant species in the various communities of *C. rutillus* territory in 1968. For each species the first two rows of figures are the dry weight per millacre (n=20) and per individual, respectively; the third row is the number of fruits per millacre (n=10) determined in the second week of August; and the fourth row, in square brackets, is the number of overwintered fruits determined in the first week of June (n=10). For stem weight the sample number is given in parentheses.

Species	White spruce	Poplar	Immature black spruce	Mature black spruce	Jackpine- juniper	Parklike jackpine
<i>G. lividum</i>	3.5 $\pm$ 0.4 0.12 $\pm$ 0.01(11) 4.4 $\pm$ 1.2	4.1 $\pm$ 0.9 0.11 $\pm$ 0.01 (8) 4.2 $\pm$ 1.2	1.3 $\pm$ 0.5 0.10 $\pm$ 0.007 (6) nil	1.4 $\pm$ 0.4 0.08 $\pm$ 0.005(7) 1.3 $\pm$ 0.4	1.2 $\pm$ 0.4 0.10 $\pm$ 0.01 (6) 6.9 $\pm$ 1.6	
<i>F. virginiana</i>	0.45 $\pm$ 0.19 0.032 $\pm$ 0.005(8) 3.5 $\pm$ 0.8				0.31 $\pm$ 0.12 0.19 $\pm$ 0.07 (8) 1.3 $\pm$ 0.6	
<i>S. canadensis</i>	23.6 $\pm$ 6.5 9.13 $\pm$ 3.7 (7) trace	34.8 $\pm$ 9.9 6.0 $\pm$ 1.2 (7) 3.3 $\pm$ 1.6			22.0 $\pm$ 8.2 3.64 $\pm$ 0.42 (8) 0.2 $\pm$ 0.1	30.3 $\pm$ 7.28 6.0 $\pm$ 1.40 (6) 0.2 $\pm$ 0.04
<i>V. vitis-idaea</i>			12.6 $\pm$ 3.35 0.10 $\pm$ 0.021(17) nil [nil]	226.4 $\pm$ 31.6 0.13 $\pm$ 0.04(20) 21.3 $\pm$ 2.6 [1.1 $\pm$ 0.5]	4.52 $\pm$ 2.20 0.1 $\pm$ 0.022 (9) 3.3 $\pm$ 0.5 [0.1 $\pm$ 0.1]	
<i>A. uva-ursi</i>		18.2 $\pm$ 1.6 0.80 $\pm$ 0.046(5) nil [nil]			177.0 $\pm$ 20.4 0.61 $\pm$ 0.032(20) 2.0 $\pm$ 0.7 [1.1 $\pm$ 0.5]	572.3 $\pm$ 87.6 0.80 $\pm$ 0.031(20) 93.8 $\pm$ 14.7 [31.7 $\pm$ 7.5]
<i>R. woodsii</i>	12.8 $\pm$ 2.3 1.42 $\pm$ 0.25(12) 0.1 $\pm$ 0.1 [trace]	62.3 $\pm$ 7.8 2.40 $\pm$ 0.19(20) 6.8 $\pm$ 2.4 [trace]		23.4 $\pm$ 4.3 1.16 $\pm$ 0.32(15) trace [trace]	4.53 $\pm$ 0.76 0.24 $\pm$ 0.02 (16) trace [trace]	55.0 $\pm$ 7.19 2.43 $\pm$ 0.18 (20) trace [trace]



Table 7. The production of important plant species in the various communities of *C. gapperi* territory in 1968. See caption of Table 6 for explanation.

Species	White spruce	Poplar	Immature black spruce	Jackpine-juniper	Parklike jackpine
<i>G. lividum</i>	0.10± 0.036 0.10± 0.001(8) nil		2.2 ±0.31 0.09 ±0.001(16) nil		
<i>F. virginiana</i>		trace ----- nil		0.28 ± 0.19 0.11 ± 0.01 nil	(4)
<i>S. canadensis</i>	1.4 ± 0.3 3.7 ± 1.43 (2) nil	689.0 ± 85.0 26.0 ± 2.2 (17) 22.0 ± 6.8		13.6 ± 4.66 13.2 ± 7.3 nil	5.1 ± 1.0 0.85± 0.01 (11) nil
<i>V. vitis-idaea</i>			9.1 ±1.65 0.10±0.019(15) nil [nil]		34.9 ± 8.47 0.20± 0.034 (8) 5.2 ± 1.0 [6.7 ± 2.1]
<i>A. uva-ursi</i>		16.5 ± 4.66 0.80 ± 0.031(13) nil [nil]		156.1 ±30.0 1.6 ± 0.042(19) 10.3 ± 6.8 [nil]	163.9 ±32.0 0.64± 0.031(18) 2.1 ± 0.84 [trace]
<i>R. woodsii</i>	1.2 ± 0.18 0.5 ± 0.05(14) nil [nil]	136.3 ± 18.8 2.4 ± 0.23 (19) 2.6 ± 1.06 [nil]		6.7 ± 1.02 0.3 ± 0.11 nil [nil]	14.7 ± 3.6 2.2 ± 0.22 (11) nil [nil]



jackpine stands which were the most productive for this fruit. Note was made on August 4, 1968 of the abundance of *Russula* sp. in the jackpine-juniper biotope of *C. rutilus* territory and its scarcity on other sites.

Although the white spruce community of *C. gapperi* territory lacked fruits, many grew and persisted in its complement. White spruce was the only stand in *C. gapperi* territory besides immature black spruce which contained *G. lividum*, although that species had a lower ( $p < 0.01$ ) biomass per area than the next richest habitat in the entire study area. None of the fruits of this species survived beyond the first week of August, however.

Of the poplar forests the one in *C. rutilus* territory produced *G. lividum* fruits, whereas that of *C. gapperi* territory was marked by amounts of *S. canadensis* which was superior ( $p < 0.05$ ) in the study area in total and individual biomass as well as in number of surviving fruits (the *C. gapperi* stand was second in importance). Most fall fruits of *R. woodsii* were found in poplar stands ( $p < 0.05$ ) where numbers were measurable, and hardly any elsewhere. No *A. uva-ursi* persisted long in these forests.

Besides small numbers of *S. canadensis* fruits, the parklike jackpine stands supplied mainly overwintering fruits. The greatest quantities ( $p < 0.05$ ) of *A. uva-ursi* fruits of the study area were produced in the stand in *C. rutilus* territory. Also, many more of these berries overwintered there ( $p < 0.001$ ) than anywhere else.

The mature black spruce community produced the largest crops of *V. vitis-idaea* fruits by far ( $p < 0.001$ ), and these overwintered in great quantities. *F. virginiana*, *S. canadensis* and *A. uva-ursi* did not grow in black spruce stands.

The immature black spruce communities, which were similar in floristic





composition, contained only *G. lividum* and *V. vitis-idaea* of the species listed in Tables 6 and 7. No fruits were retained until the second week of August.

Cover. Although vegetative growth was highest in 1966 cover remained relatively constant from year to year (Table 8). Since no differences were found between spring and fall values for any aspect of cover these values are combined in Table 9 to better show biotopic variation.

The concentration of fallen trees (Table 9) was highest in the *C. rutilus* sites for almost every forest type. There was great (often significant) variation in this aspect in both sites between the generally high values of white spruce, poplar and jackpine-juniper, and the low ones of black spruce and parklike jackpine. The *nature* of these logs varied also. None found in the three muskeg sites were large, but most of those in the parklike jackpine, and some in the white spruce areas, were large and, because they still retained their branches, were often slightly elevated from the forest floor. Those of the other sites were similar in that they lay flat and varied in size.

Litter, like fallen trees, was scarcest in the muskegs and parklike stands where it had no value as rodent shelter (Table 9). The abundant litter of the poplar stands, caused by annual defoliation of the dominants, decreased in utility throughout the growing season because of fragmentation. The amount in white spruce and jackpine-juniper was second largest, but only the former had litter of value as cover.

Of the foliage cover (Table 9), especially notable is the tremendous difference between the best sites and those lacking understory (the parklike stands and white spruce of *C. gapperi* territory). The leaf cover of *C. rutilus* white spruce, the muskegs and the jackpine-juniper stands were judged to be



Table 8. Annual comparisons (mean  $\pm$  S.E.) of three aspects of cover in three biotopes of *C. rutilus* territory. Measurements were made at the same time as those of aerial biomass. 1=white spruce, 2=mature black spruce, 3=jackpine-juniper. The sample number is 10 in all cases.

Cover	Site	1965		1966		1967	
Fallen trees (No. per millacre)	1	3.3	0.6	3.6	0.6	2.2	0.8
	2	1.9	0.5	1.3	0.4	1.5	0.3
	3	-----		4.4	0.6	3.7	0.5
Litter (% by area)	1	59.0	6.5	68.5	5.8	53.3	9.4
	2	14.9	8.8	10.1	5.0	10.8	2.9
	3	-----		47.2	5.4	46.9	9.5
Foliage cover (% by area)	1	25.6	3.5	28.1	2.0	26.8	8.8
	2	50.4	5.2	65.0	3.6	51.3	4.4
	3	-----		20.0	3.1	26.6	3.9



Table 9. Biotopic comparisons (mean  $\pm$  S.E.) of three aspects of cover in 1968. All values are averages of 20 estimates.

Type and Area	White spruce	Poplar	Immature black spruce	Mature black spruce	Jackpine- juniper	Parklike jackpine
<i>C. rutilus</i> area						
Fallen trees (No. per millacre)	2.7 $\pm$ 0.7	3.0 $\pm$ 0.4	0.1 $\pm$ tr	1.6 $\pm$ 0.2	4.0 $\pm$ 0.4	1.2 $\pm$ 0.2
Litter (% by area)	63.2 $\pm$ 4.3	62.9 $\pm$ 5.2	8.4 $\pm$ 1.0	15.0 $\pm$ 4.1	50.0 $\pm$ 5.2	25.3 $\pm$ 5.2
Foliage cover (% by area)	27.0 $\pm$ 2.4	29.6 $\pm$ 2.0	21.1 $\pm$ 2.7	56.0 $\pm$ 3.4	23.2 $\pm$ 2.9	4.9 $\pm$ 0.7
<i>C. gapperi</i> area						
Fallen trees (No. per millacre)	2.6 $\pm$ 0.6	1.1 $\pm$ 0.2	0.5 $\pm$ 0.2		0.6 $\pm$ 0.2	0.4 $\pm$ 0.1
Litter (% by area)	26.2 $\pm$ 5.0	51.3 $\pm$ 5.2	3.0 $\pm$ 0.6		25.4 $\pm$ 4.3	10.2 $\pm$ 1.4
Foliage cover (% by area)	5.1 $\pm$ 0.7	48.2 $\pm$ 6.3	19.3 $\pm$ 2.5		16.7 $\pm$ 2.0	5.1 $\pm$ 0.7





the most suitable for rodent shelter.

Summary and discussion. Generally, 1965 and 1966 were characterized by early advents and copious production of leaves and fruits, the potential plant foods for the animals of this study. In fact, the large fruit production of 1966 warrants designating that year a "fruit year."

In contrast, 1967 and 1968 showed delayed phenologies, reduced vigor of vegetation and small fruit crops. These years differed, however, in availability of overwintered fruits in early summer. As a result of the bumper crop of 1966 there was a large carryover to the spring of 1967, whereas the poor production of 1967 provided few overwintered berries for the spring of 1968. There also appeared to be a resurgence of certain ephemeral fruits in 1968, especially *F. virginiana*.

These data may be explained in terms of weather conditions (Figs. 15 and 16) and Kalela's (1962) suggestion that two years are necessary to produce a bumper crop. Thus, conditions in 1965 allowed the production of many fruit primordia, and the climatically favorable summer of 1966 enabled these to develop abundantly. Another rich crop of buds in 1966 failed to materialize in 1967 because of the prolonged cold prevernal period which was reflected also in the phenological lag and reduced vigor. Because of the production of few primordia in 1967, and the unfavorable conditions in early summer of 1968, the crop of 1968 was also low and that of 1969 may be predicted to be similar. Fuller (*pers. comm.*) reported a favorable spring in 1969 and a large crop on the study area in 1970 as opposed to 1969. *F. virginiana* showed a similar time span between major crops but, because it was out of phase with the species discussed above, may be independent of weather effects. Observations outside the study plots suggested that *R. oxyacanthoides* may behave similarly.



The shortage of berries in 1967 and 1968 was compensated for in terms of cricetid food by the mushroom crop which peaked in 1967 when precipitation was 70 mm higher than normal, and which was almost as plentiful in 1968 when rainfall was 35 mm higher than normal (Fig. 16). It is notable in this regard that the wet year of 1964 produced a memorable mushroom crop (Mr. William Clark, *pers. comm.*). Mushrooms, unfortunately, in contrast to overwintering fruits, are of no value outside of the fruiting season.

Earlier phenological advents and a seemingly higher fruit production in more open sites may be, at least in part, due to varying light penetration and snow persistence. Spatial variation in disappearance of fruit crops may also have been dependent on exposure, probably to frugivores. Vegetative production appeared to be abundant in all sites, but fruit production varied greatly in kind and degree. Of the areas examined, those in *C. gapperi* territory were generally less successful in fruit retention, if not in production, and the immature bogs had the fewest fruits at all times.

Cover varied in quantity and quality only spatially. The only habitats lacking in all three types of cover were the parklike jackpine stands. But for fallen trees the white spruce of *C. gapperi* territory was also notably lacking in cover. Except for foliage cover, which existed only at the lowest levels, so were the immature muskegs. The poplar stands showed the greatest overall cover potential.

### Food Preference

Values for the *passage* index are generally centred on 50, suggesting random visitations to the two chambers (Fig. 23). It is therefore useless except for the grossest distinctions (e.g., fruits versus stems). The





Figure 23. Preference according to *passage* index for several foods available during the fruiting season. The mean, standard error, standard deviation, range and sample number are shown. Guide lines are drawn at the 50% level. High values indicate high preferences.



"PASSAGE" INDEX →

LICHENS:

- Cladonia* spp.
- Peltigera* spp.

FUNGI:

- Hydnum* sp.
- Sarcodon* sp.
- Russula* sp.

BRYOPHYTES:

- Sphagnum* spp.
- Hypnum splendens*

GRAMINOIDS:

- Calamagrostis inexpectata*

TRACHEOPHYTE STEMS:

- Arctostaphylos uva-ursi*
- Vaccinium vitis-idaea*
- Fragaria virginiana*
- Geocaulon lividum*

TRACHEOPHYTE LEAVES:

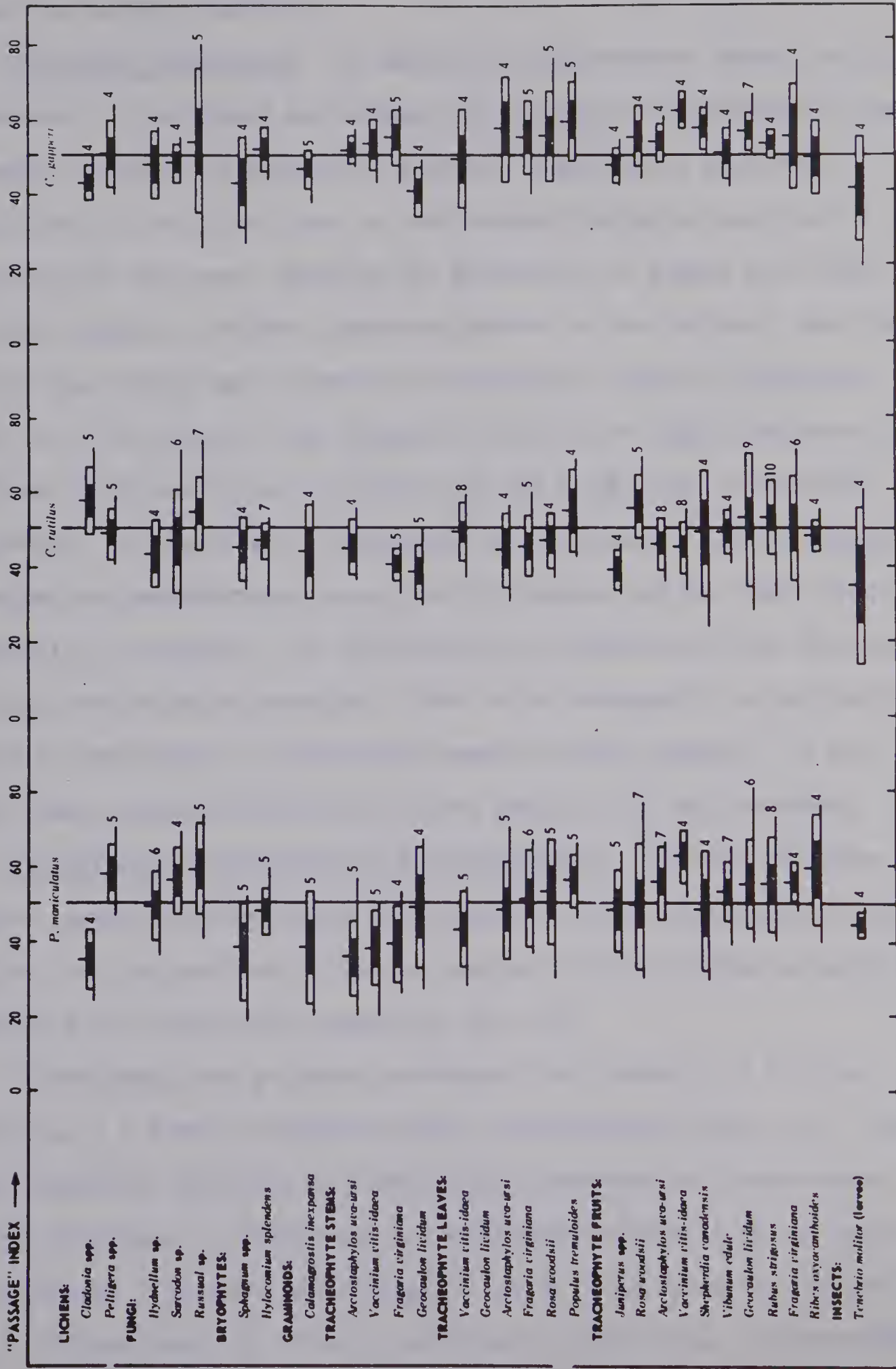
- Vaccinium vitis-idaea*
- Geocaulon lividum*
- Arctostaphylos uva-ursi*
- Fragaria virginiana*
- Rosa woodsii*
- Populus tremuloides*

TRACHEOPHYTE FRUITS:

- Juniperus* spp.
- Rosa woodsii*
- Arctostaphylos uva-ursi*
- Vaccinium vitis-idaea*
- Shepherdia canadensis*
- Viburnum edule*
- Geocaulon lividum*
- Rubus strigosus*
- Fragaria virginiana*
- Ribes oxycanthoides*

INSECTS:

- Tenebrio molitor* (larvae)





*time* index (Fig. 24) is more sensitive, but the *weight* index (Fig. 25) appears to be most sensitive.

Individual preferences. In addition to experimental error, individual differences in preference may account for dispersion of preference values. To assess relative, as opposed to absolute, dispersion I used the Coefficient of Variation; that is, the standard deviation expressed as a percentage of the mean. Ignoring the differences in sample size which, for small samples, can have tremendous effects on the variance, the *time* indices show hardly any variation in dispersion—relative or absolute (Fig. 24). The apparent high dispersion of the more highly preferred foods of Figure 25 is deceiving since there are few differences in *relative* dispersion. Of the rodents, *Peromyscus* had the lowest relative dispersion of values for mealworm preferences and the highest for the fruits (note, especially, *R. woodsi*). For this rodent, the higher the fruit preference the lower the relative variation. This is not necessarily so for the voles. Otherwise, there were no differences among the three species. In all three groups mushroom preferences varied greatly with the individual.

Comparisons of preference in fruiting season. Although the three rodents showed peculiarities of preference as well as some general resemblances, the similarities of the two species of *Clethrionomys* as opposed to *Peromyscus* are obvious (see especially Fig. 25).

*Clethrionomys* has a greater preference for lichens ( $p < 0.05$  for *Peltigera*;  $p < 0.001$  for *Cladonia*) than does *Peromyscus* (Fig. 25). The other vegetative foods are also more highly preferred by *Clethrionomys* than by *Peromyscus*. Differences are significant according to the *weight* index between *C. gapperi* and *Peromyscus* for *V. vitis-idaea*, *A. uva-ursi* and *G. lividum* stems ( $p < 0.05$ ); and between *Clethrionomys* and *Peromyscus*





Figure 24. Preference according to *time* index for several foods available during the fruiting season. The mean, standard error, standard deviation, range and sample number are shown. Guide lines are drawn at the 40% level.



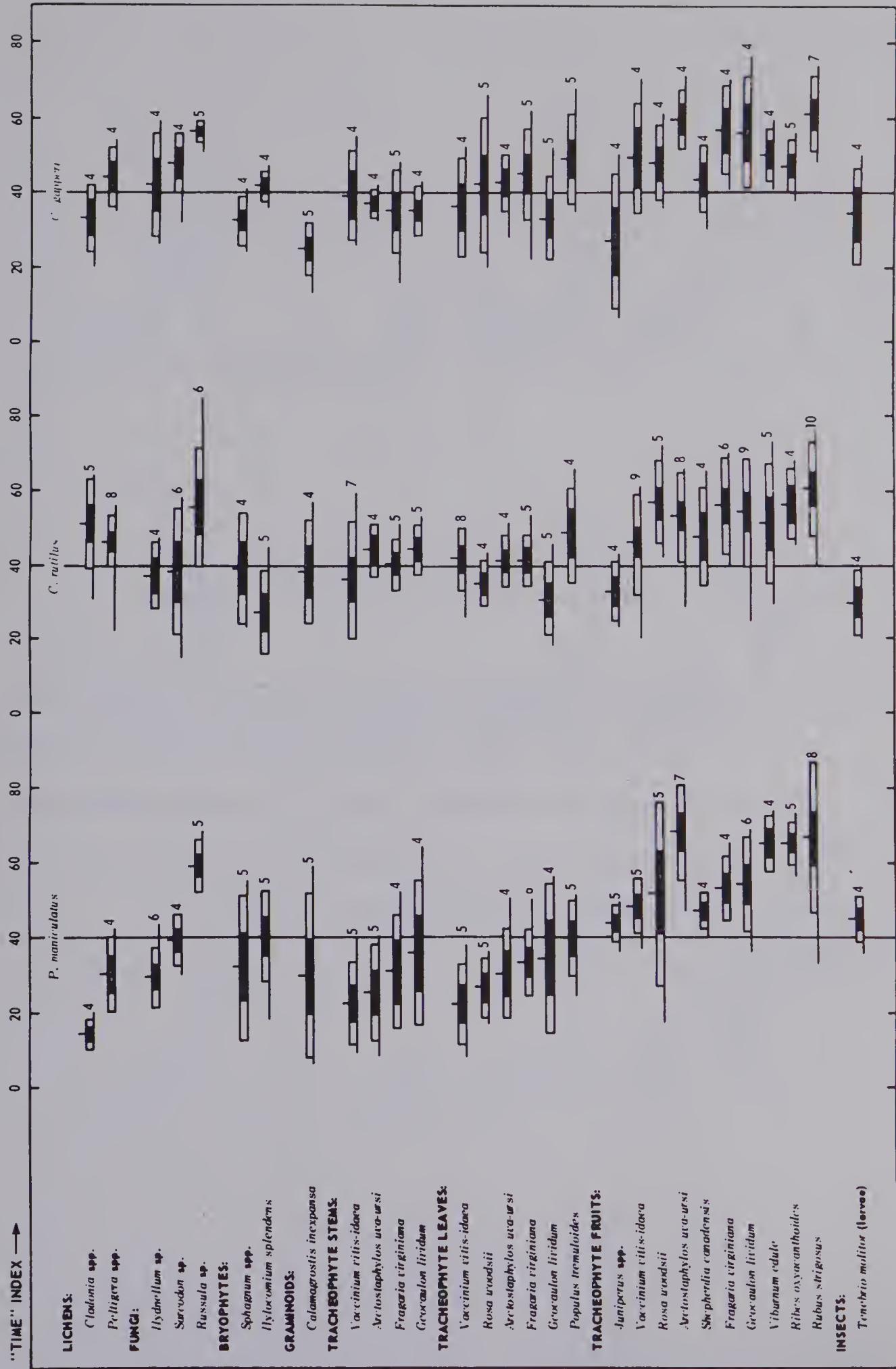
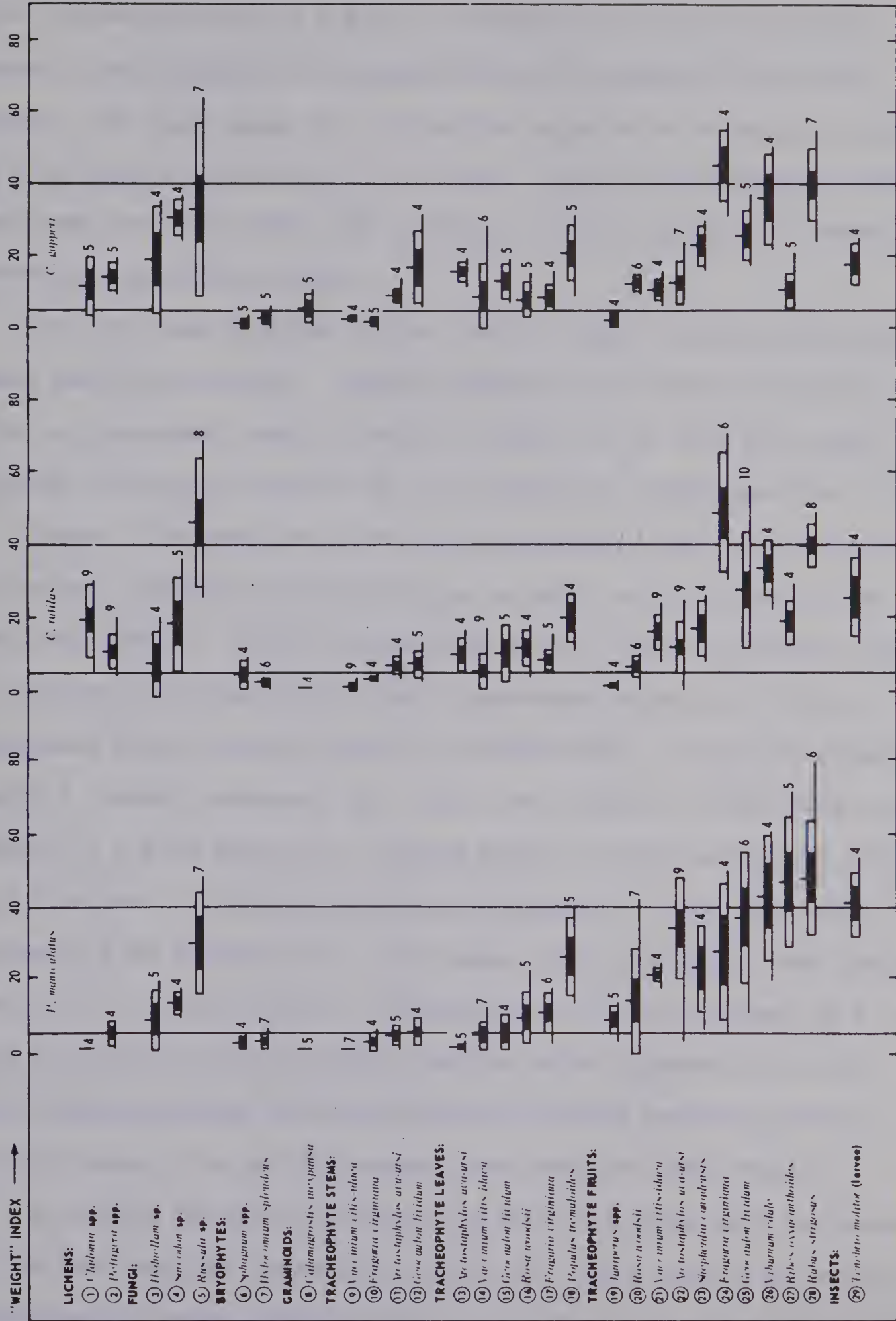






Figure 25. Preference according to *weight* index for several foods available during the fruiting season. The mean, standard error, standard deviation, range and sample number are shown. Guide lines are drawn at the 5 and 40% level. The encircled numbers are used in Figure 27







for *A. uva-ursi* leaves ( $p < 0.05$ ). *Calamagrostis inexpansa* was only eaten in small amounts by *C. gapperi* and was not eaten at all by the others. The woody stems of *V. vitis-idaea* appeared to be totally unpalatable to deermice, and nearly so to voles. In all three rodents the more succulent stems and leaves were preferred, and the values of *P. tremuloides* leaves were particularly high.

For the three mushrooms tested, indices suggest similar preferences among the three cricetids. Highest preferences are shown for *Russula* sp. (the most succulent) and the lowest for *Hydneillum* sp. (the most woody), although the *weight* index did not show significant differences for *C. gapperi*.

Fruits, like mushrooms, were highly preferred by all three species. An obvious exception was *Juniperus* spp. in which only the flesh of the fruit was nibbled. Of the overwintering fruits, those of *Juniperus* and *A. uva-ursi* gave significantly higher preference values ( $p < 0.05$ ) in *Peromyscus* than in the two species of *Clethrionomys*. *C. gapperi* showed a higher *R. woodsii* preference ( $p < 0.05$ ), but a lower *V. vitis-idaea* preference ( $p < 0.05$ ) than did *C. rutilus* which, in turn, had a lower value ( $p < 0.05$ ) for *V. vitis-idaea* than did *Peromyscus*. It was noted that voles ate more of the ectocarp of *V. vitis-idaea* fruits, while all three species ate seeds to the same extent. The same amounts of the ectocarps of *A. uva-ursi* were eaten by mice and voles, but the latter appeared to eat less seed contents and more of the mealy flesh (mice ate greater quantities in absolute terms). No such differences were noted for other fruits.

*R. woodsii* had the only fruits from which the seeds could be separated to test the individual plant parts (Table 10). Seed content was eaten in significantly lesser quantities than was the flesh of the fruit ( $p < 0.005$  for *Peromyscus*:  $p < 0.001$  for *Clethrionomys*). The time index, however,



Table 10. Comparisons of preference values (mean  $\pm$  S.E.) obtained for fruits of *Rosa woodsii* and the achenes and flesh of these during the fruiting season. The sample number is given in parentheses.

Species and Indices	Whole	Flesh	Seed
<i>P. maniculatus</i>			
Passage	49.7 $\pm$ 6.2(7)	70.9 $\pm$ 1.3(2)	64.6 $\pm$ 10.3(2)
Time	51.6 $\pm$ 11.0(5)	49.4 $\pm$ 3.0(2)	41.2 $\pm$ 21.1(2)
Weight	14.0 $\pm$ 5.6(7)	19.8 $\pm$ 3.5(4)	8.0 $\pm$ 2.5(4)*
<i>C. rutilus</i>			
Passage	55.9 $\pm$ 4.7(5)	50.5 $\pm$ 4.6(5)	46.1 $\pm$ 2.6(5)
Time	57.0 $\pm$ 5.0(5)	47.3 $\pm$ 7.3(5)	61.3 $\pm$ 5.0(5)
Weight	6.7 $\pm$ 1.5(6)	14.6 $\pm$ 5.1(6)	4.1 $\pm$ 1.1(6)**
<i>C. gapperi</i>			
Passage	55.0 $\pm$ 5.4(4)	59.6 $\pm$ 8.1(3)	39.2 $\pm$ 7.4(3)
Time	47.6 $\pm$ 5.1(4)	46.5 $\pm$ 6.5(3)	47.2 $\pm$ 8.1(3)
Weight	12.7 $\pm$ 0.06(6)	23.3 $\pm$ 4.1(3)	3.4 $\pm$ 1.0(5)**

\*Significantly less (p < 0.05) than the former category.  
\*\*Highly significantly less (p < 0.001) than the former category.



does not show the differences; perhaps because seeds must be broken into and the contents removed, whereas flesh is readily accessible.

In Figures 23-25 the preference values of the different categories are arranged in increasing order for *Peromyscus*. In the weight index only, this arrangement has forced the ephemeral fruit preferences into similar patterns for the two voles, but these showed preferences distinct from those of the mice (Fig. 25). Except in the case of *F. virginiana*, all values were generally lower in *Clethrionomys*, although significantly so ( $p < 0.05$ ) only in the case of the fruits of *R. oxyacanthoides*.

Seasonal preference changes. Seasonal comparisons of preference for some vegetative plant parts which were plentiful and cosmopolitan are given in Table 11. Although no winter values were obtainable for *C. rutilus* there is indication that the cricetids, especially *C. gapperi*, had high preferences for ground lichens in winter. The drop in spring was significant ( $p < 0.05$  by the *time* index;  $p < 0.001$  by the *weight* index) for *Cladonia* spp. in *C. gapperi*. In *Peromyscus*, of which only two individuals were obtainable in winter, the drop was only significant ( $p < 0.05$  by both *time* and *weight* indices) for *Cladonia* spp. in autumn at which time its preference for *Peltigera* spp. increased.

*Peromyscus* showed its highest preference (not significant) for feather moss in the spring, while *C. gapperi* had a high winter preference which dropped throughout the spring to a significant low ( $p < 0.05$ ) in the fruiting season. *C. rutilus* preference for this food decreased significantly ( $p < 0.025$ ) throughout the summer.

There are no significant seasonal differences between values for stems and leaves of *V. vitis-idaea*. In *C. rutilus* only, stems and leaves of *F. virginiana* were tested in early summer as well as in the fruiting





Table 11. Comparisons of preference values (mean  $\pm$  S.E.) obtained for some common vegetative plant foods in three different seasons. The two indices are *time* and *weight* reading from top to bottom. The sample numbers are given in parentheses.

Subjects and Foods	Feb.-Mar., 1967	May-June, 1967-68	Sept.-Oct., 1967-68
<i>Peromyscus</i>			
<i>Cladonia</i> spp.	20.0 $\pm$ 1.9(2) 2.0 $\pm$ 1.4(2)	22.4 $\pm$ 6.8(5) 1.4 $\pm$ 0.4(6)	11.4 $\pm$ 0.5(2)* 0.0 $\pm$ 0.0(4)*
<i>Peltigera</i> spp.	27.0 $\pm$ 14.3(2) 0.4 $\pm$ 0.2(2)	22.5 $\pm$ 5.1(6) 0.1 $\pm$ 0.1(6)	29.8 $\pm$ 6.7(2) 4.1 $\pm$ 2.0(4)*
Feather mosses	41.9 $\pm$ 26.8(2) 1.5 $\pm$ 1.4(2)	37.7 $\pm$ (1) 6.5 $\pm$ 1.1(2)	39.5 $\pm$ 5.6(5) 3.0 $\pm$ 0.9(7)
<i>V. vitis-idaea</i> (stems)	16.3 $\pm$ 4.2(2) 0.0 $\pm$ 0.0(2)	18.7 $\pm$ 5.4(2) 0.0 $\pm$ 0.0(2)	21.8 $\pm$ 5.1(5) 0.0 $\pm$ 0.0(7)
<i>V. vitis-idaea</i> (leaves)	23.9 $\pm$ 6.5(2) 0.0 $\pm$ 0.0(3)		21.9 $\pm$ 5.3(5) 4.0 $\pm$ 1.6(7)†
<i>C. rutilus</i>			
<i>Cladonia</i> spp.		29.7 $\pm$ 5.0(2) 11.9 $\pm$ 2.1(2)	52.6 $\pm$ 6.4(5) 20.5 $\pm$ 3.8(6)
<i>Peltigera</i> spp.		28.0 $\pm$ 6.0(2) 4.8 $\pm$ 0.9(2)	44.1 $\pm$ 4.0(5) 8.6 $\pm$ 1.2(6)
Feather mosses		35.6 $\pm$ 0.4(2) 3.7 $\pm$ 0.3(2)	27.3 $\pm$ 5.0(5) 1.4 $\pm$ 0.4(6)*
<i>V. vitis-idaea</i> (stems)		30.4 $\pm$ 7.9(2) 1.0 $\pm$ 0.7(2)	35.9 $\pm$ 6.3(7) 0.8 $\pm$ 0.5(7)
<i>V. vitis-idaea</i> (leaves)			40.8 $\pm$ 3.5(7) 6.0 $\pm$ 2.3(7)
<i>C. gapperi</i>			
<i>Cladonia</i> spp.	37.8 $\pm$ 3.8(4) 17.0 $\pm$ 3.2(5)	19.7 $\pm$ 4.3(7)* 3.9 $\pm$ 1.4(7)**	33.0 $\pm$ 6.7(3) 13.4 $\pm$ 5.0(5)
<i>Peltigera</i> spp.	33.6 $\pm$ 4.1(5) 12.8 $\pm$ 0.9(5)	37.0 $\pm$ 5.2(5) 7.2 $\pm$ 7.8(5)	47.0 $\pm$ 7.0(2) 11.6 $\pm$ 3.4(5)
Feather mosses	44.0 $\pm$ 2.0(4) 7.3 $\pm$ 1.4(4)	43.0 $\pm$ 1.4(5) 4.2 $\pm$ 1.0(5)	43.6 $\pm$ 2.0(3) 3.0 $\pm$ 1.1(5)†
<i>V. vitis-idaea</i> (stems)	40.6 $\pm$ 6.5(5) 2.3 $\pm$ 1.0(5)	42.6 $\pm$ 5.5(5) 3.7 $\pm$ 1.2(5)	46.0 $\pm$ 9.0(2) 2.6 $\pm$ 0.2(4)
<i>V. vitis-idaea</i> (leaves)	36.8 $\pm$ 2.2(5) 2.4 $\pm$ 0.7(5)		36.0 $\pm$ 7.5(4) 4.6 $\pm$ 1.9(4)

\*Significantly different ( $p < 0.05$ ) from the preceding season.

\*\*Highly significantly different ( $p < 0.001$ ) from the preceding season.

†Fall significantly different ( $p < 0.05$ ) from late winter.



season, but because of the lack of significant changes these values were combined in Figures 23-25.

*Overwintered* versus *fresh* preference values for the four main overwintering fruits are compared in Figure 26. Because *C. rutilus* were not trappable when the spring tests were being performed in 1967, and because overwintered fruits were not available in the spring of 1968 when two *C. rutilus* subjects were caught in late winter, values for this species are not given in the figure.

*Peromyscus* preferred the fresh fruits at the end of the summer to their overwintered counterparts in the spring (Fig. 26). *C. gapperi* had equally low preferences for *Juniperus* and *R. woodsii* fruits in both spring and fall, and otherwise a lower (extremely so in the case of *V. vitis-idaea* fruits) preference for the new fruits. It is suspected, therefore, that *Peromyscus* prefers these fruits less after they have overwintered, especially *A. uva-ursi*. *C. gapperi* has equal seasonal reliance on the two less preferred overwintering fruits and, of the others, *V. vitis-idaea* berries may be especially important at other times than the fruiting season. *C. rutilus* seasonal preference changes, which were not determined, are assumed to resemble those of *C. gapperi* rather than those of *Peromyscus*.

Critique of method. The extent of some of the observed dispersions indicates that preference methods involving one or two tests are not valid.

Of the methods employed in this study there are no differences among the three in variance size for highly preferred foods, suggesting that discreteness is a virtue of the *weight* index only for relatively unsavory foods.

In Figure 27 the values of Figure 24 are plotted against those of





Figure 26. Comparisons of spring and fall preference values for the four main overwintering fruits in *Peromyscus* and *C. gapperi*. The mean, standard deviation, range and sample number are shown. The solid arrows indicate a significant change in preference at least at the 5 per cent level.



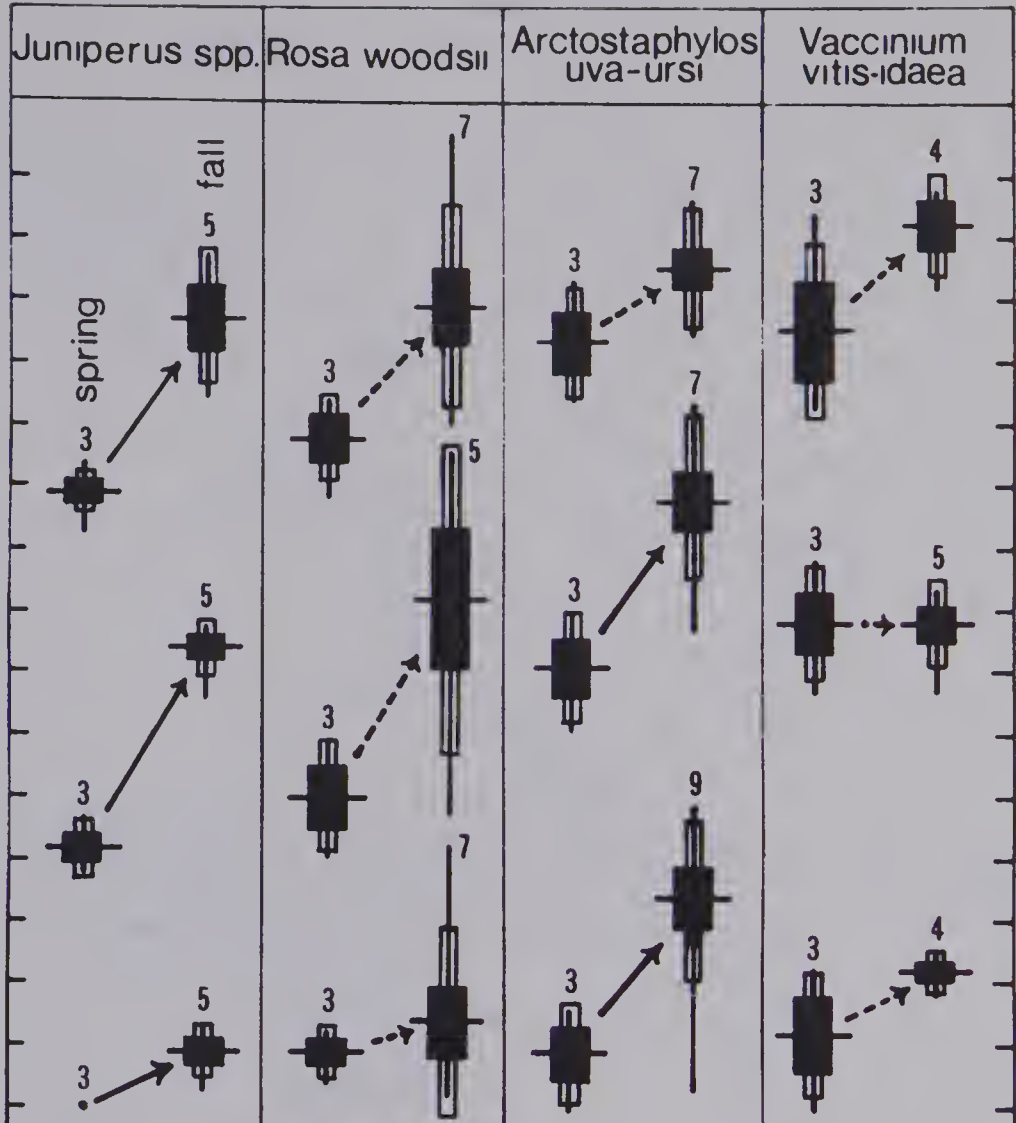
*P. maniculatus*

PASSAGE

TIME

WEIGHT

70  
60  
50  
40  
30  
20  
60  
50  
40  
30  
20  
10  
30  
20  
10  
0



*C. gapperi*

PASSAGE

TIME

WEIGHT

70  
60  
50  
40  
30  
50  
40  
30  
20  
50  
40  
30  
20  
10  
0

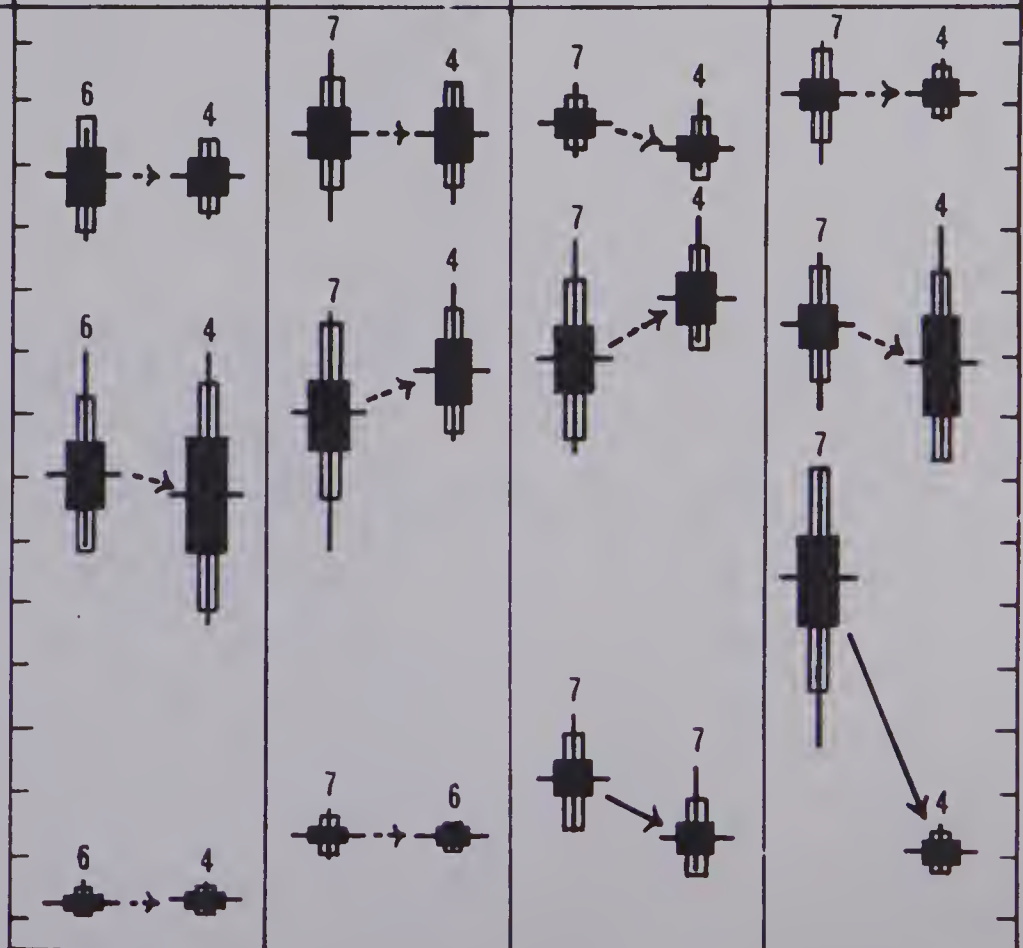






Figure 27. *Time* index plotted against *weight* index for several foods available during the fruiting season. The numbers refer to the foods of Figure 25.

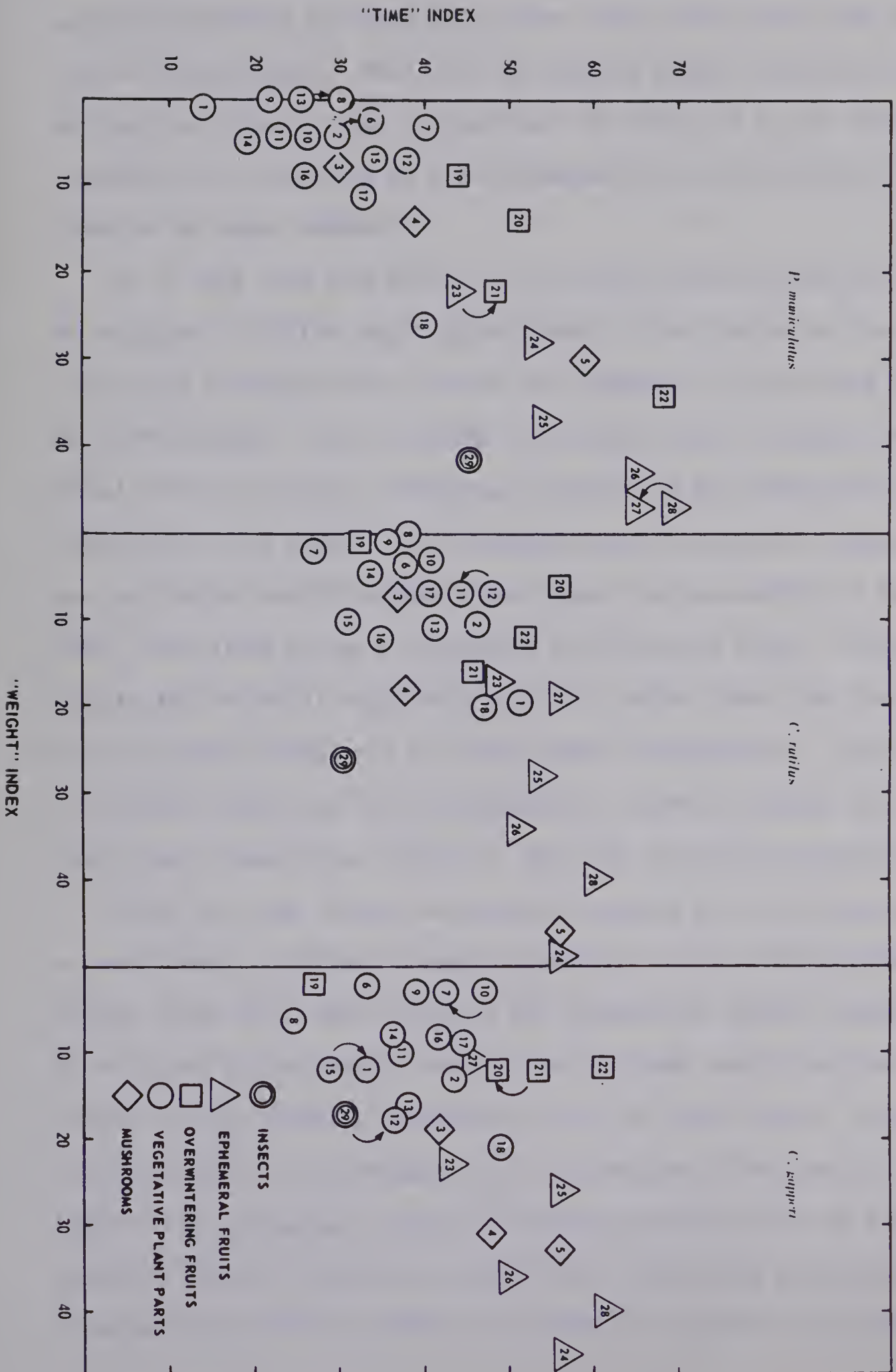






Figure 25. An imaginary fitted line would indicate a linear relationship and would intersect the axis of the *time* index—well above zero in the case of *Clethrionomys*. Thus, the two indices roughly substantiate one another, but there is some "attraction" for food even in the absence of "palatability" (according to pilot observations, this "attraction" is not shown for an empty chamber).

As is best seen from Figure 27, the *weight* index values for all three animals span a similar range (approximately 0-50%) while the *time* index values span a range of 60% (10-70%) for *Peromyscus* but only 40% (20-60%) for *Clethrionomys*. Thus, although the *weight* index is roughly the same for all three cricetids, *Peromyscus* is unique in the comparatively wide scope of its *time* index. For *Peromyscus*, both the higher concordance of the two indices and the higher slope depict the superiority of the *time* index, both alone and as a reflection of the *weight* index. Therefore, despite the universal applicability of the *weight* index, the *time* index must be applied cautiously to "inter-rodent" comparisons. Since weights of different foods may not be commensurate, another drawback exists for "inter-food" comparisons (except in the case of seasonal comparisons).

Since the same subject was usually employed for the bioassay of two or more foods, a problem of sample dependency exists for comparisons between foods which does not exist for comparisons between rodents. But, as witnessed by the unequal sample sizes, animals were often lost or replaced, so that complete dependency is not the case either. Supposing a cancellation of the advantages of the two methods of determining statistical significance (assuming a positive correlation between any two sets of data, dependent samples should more readily show significant differences: alternatively, twice the number of degrees of freedom are available when



independent samples are compared), the present dilemma was resolved by treating all samples as independent.

### Maintenance Values

When foods used in the preference tests were fed singly to the animals *ad libitum*, they survived from 2 to 63 days and lost weight at rates of zero to 12 per cent of their original weight per day (Table 12). For convenience of comparison, major categories are arranged in Table 12 in order of decreasing weight loss values; arboreal lichens, which the natural consumption surveys showed to be of importance, are added to the list. Relative lack of longevity values in the table is owing to my reluctance to allow animals to starve.

*P. maniculatus* maintained its weight best on the more succulent mushrooms and most of the fruits; and slightly less successfully on *R. woodsii* fruits, woody mushrooms, succulent leaves and arboreal lichens (Table 12). Weight was lost rapidly on *Juniperus* fruits, ground lichens, moss, waxy-cuticled leaves and succulent stems. Woody stems were not used because their low preference would doubtless have caused precipitous starvation.

*Clethrionomys* spp. showed similar regimens with a few exceptions (Table 12). Mushrooms (including *Hydnellum* sp.) were more successful ( $p < 0.05$ ) in maintaining weight in *Clethrionomys* than in *Peromyscus*, and fruits were generally a little less successful ( $p < 0.05$  in the case of *A. uva-ursi*). Weight maintenance on ground lichens was significantly higher in *C. gapperi* ( $p < 0.02$ ) than in *Peromyscus*. Also, unlike *Peromyscus*, *Clethrionomys* showed lower weight loss on *Cladonia* than on *Peltigera* ( $p < 0.05$  in *C. rutilus*). For several foods *C. gapperi* showed higher





Table 12. Results (mean  $\pm$  S.E.) of feeding various natural plant foods *ad libitum* to the subjects. Sample numbers for weight loss values are given in parentheses, and survival values are shown only for animals with unusual longevity and those allowed to starve.

Foods	<i>P. maniculatus</i>			<i>C. rutilus</i>			<i>C. gapperi</i>		
	Time until death (days)	Weight loss (% initial weight/day)		Time until death (days)	Weight loss (% initial weight/day)		Time until death (days)	Weight loss (% initial weight/day)	
Fungi:									
<i>Hydnellum</i> sp.		3.0 ± 1.0 (2)		>10, >9	0.0 (2)			0.8 (1)	
<i>Sarcodon</i> sp.		1.8 ± 0.24(2)			1.2 ± 0.30(2)	>15		0.0 (2)	
<i>Russula</i> sp.	47	1.0 ± 0.44(3)		>29, >27	0.5 ± 0.45(2)	63		0.0 (2)	
Combination		1.1 (1)		>15, >40	0.0 (2)	>10, >11		0.4 ± 0.4 (2)	
Tracheophyte fruits:									
<i>Juniperus</i> spp.		6.8 (1)			8.8 ± (1)			11.7 (1)	
<i>R. woodsii</i>		3.5 ± 0.50(2)			3.4 (1)			7.0 ± 1.0 (2)	
<i>V. vitis-idaea</i>		1.5 ± 0.50(2)			2.0 (1)			2.0 ± 1.0 (2)	
<i>A. wa-ursi</i>		1.6 ± 0.28(3)		4	4.0 ± 0.58(3)			4.0 ± 2.0 (2)	
<i>F. virginiana</i>		2.7 (1)			1.0 (1)			1.0 (1)	
<i>G. lividum</i>		3.1 ± 0.90(2)			3.5 (1)			5.0 ± 0.65(2)	
<i>R. strigosus</i>		2.0 ± 0.20(2)		>14	0.8 ± 0.20(2)			0.6 (1)	
Tracheophyte leaves:									
Heaths*		8.4 (1)			3.8 (1)			5.0 (1)	
<i>G. lividum</i>	11, 8	3.2 ± 0.41(3)			2.1 ± 0.40(2)	6		3.1 ± 0.87(3)	
<i>R. woodsii</i> and <i>F. virgin.</i>	8	3.5 ± 0.55(3)			2.4 (1)			5.0 (1)	
<i>P. tremuloides</i>	9, 9, 7, 8	3.2 ± 0.58(5)			2.1 ± 0.52(3)			1.9 ± 0.23(3)	
Arboreal lichens:									
<i>Usnea</i> sp.		4.0 ± 0.50(2)			2.0 ± 1.0 (2)			6.0 ± 3.0 (3)	
<i>Parmelia</i> sp.		5.0 (1)			1.0 (1)			3.0 (3)	
Tracheophyte stems:									
<i>F. virginiana</i>		7.6 (1)			5.6 (1)			7.2 (1)	
<i>G. lividum</i>		5.0 (1)			2.2 (1)			2.0 (1)	
Ground lichens:									
<i>Cladonia</i> spp.	3, 9, 4, 4	8.0 ± 1.56(4)		8	3.0 ± 0.82(4)	2, 3		7.0 ± 1.15(3)	
<i>Peltigera</i> spp.	6, 2	7.2 ± 1.32(4)		6	6.5 ± 1.03(2)	1, 3		12.0 ± 1.22(3)	

\**A. wa-ursi* and *V. vitis-idaea*





weight loss than *C. rutilus*.

Of the arboreal lichens, important in the natural diet, the fine, scarce *Alectoria jubata* could not be extricated from tree bark in sufficient quantity for testing. The two assayed (*Usnea* and *Parmelia*) were more successful in maintaining weight in all three rodents than were ground lichens.

Unfortunately, a functional (and, doubtless, causal) relationship existed between preference and maintenance in the present tests. It was noted, indeed, that with some foods animals starved because of a complete lack of *palatability*. To solve this problem, the means of the maintenance indices were corrected for preference using the means of the preference values of Figure 25 and the negative linear regression lines shown in Figure 28. The procedure used (Ostle, 1963) takes account of these relationships while adjusting all maintenance values to a single mean preference value (indicated in Figure 27). Where combinations of food were provided, the corresponding preferences were averaged.

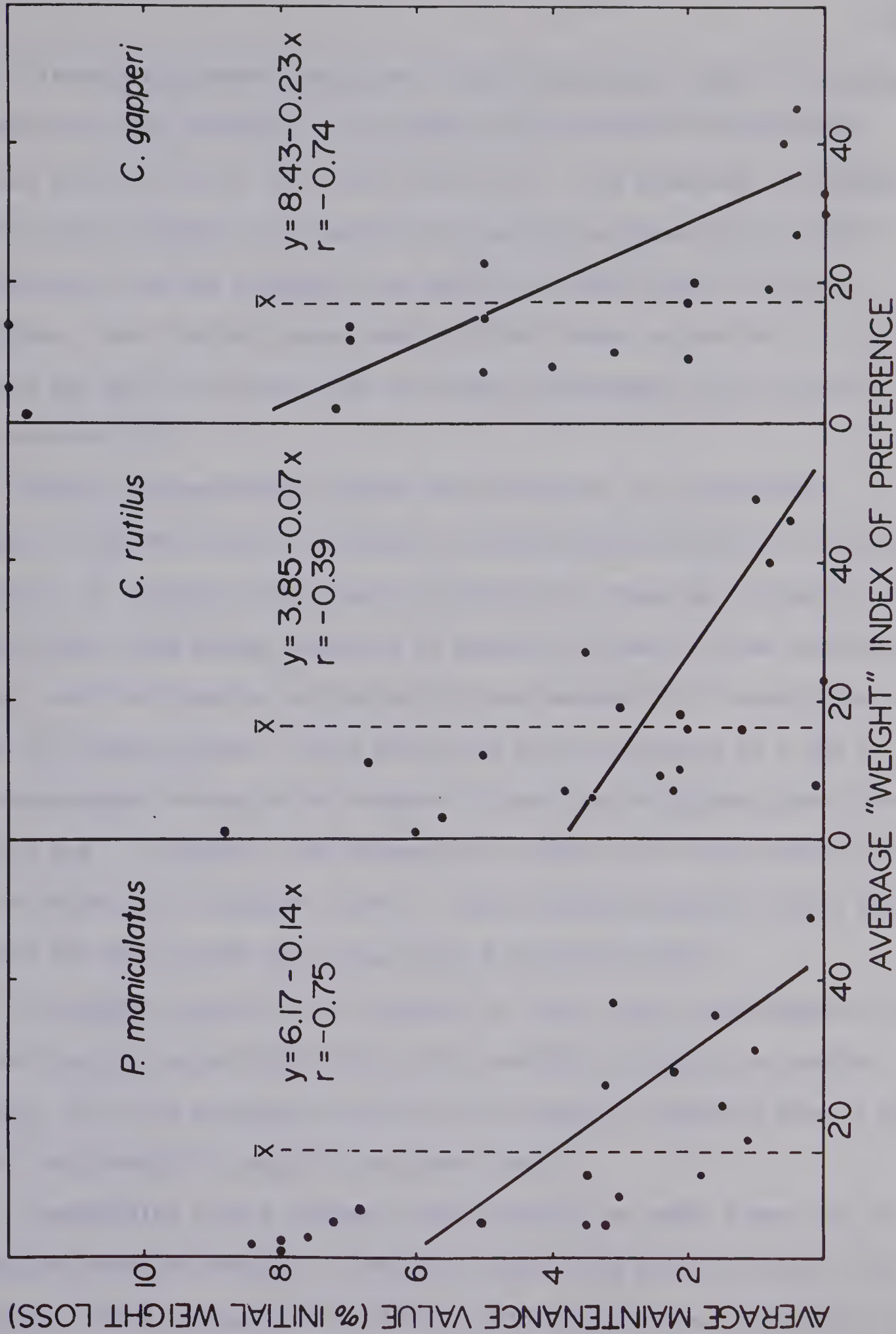
A comparison of the regression lines of the three rodents (Fig. 28) indicates some major differences. *C. gapperi* has slope and intercept values which are greater than those of *P. maniculatus* and, more surprisingly, much greater than the *C. rutilus* values. This is mainly explainable by an extraordinary ability of *C. rutilus* to survive on foods high in roughage and low in preference such as lichens, mosses and woody mushrooms. (This also explains the low correlation coefficient for this species.)

It is more difficult to account for the behavior of the regression line of *P. maniculatus*. Its low y-intersect and slope suggest that it has the ability to maintain weight on low preference foods. However, its less capacious alimentary apparatus (Fig. 1) would suggest the contrary.





Figure 28. Maintenance indices plotted against preference values for foods of the three cricetids. The broken vertical line indicates the mean preference value to which the maintenance values are adjusted in Table 13.







Although adjustment causes the values to converge (Table 13), making comparisons more difficult, alterations in the patterns of maintenance values presented above are obvious (Table 13). The gradation of mushroom worth which increased with succulence disappears as does "inter-rodent" differences, but the remarkably low indices of these fungi *in toto* is retained. Stem indices become lower and leaf values impressively so; but fruits are seen to be poor foods for weight maintenance when preference is accounted for.

Because the preference indices were not known, the maintenance values of the two species of arboreal lichens assayed could not be adjusted. However, the adjusted values may be estimated by comparing the amounts of these foods eaten during the tests to amounts of foods of known preference. Thus, *Usnea* and *Parmelia* were eaten in trace amounts by *P. maniculatus* as were the ground lichens. Since the latter have preferences of 0 and 5, the maintenance values of the arboreal lichens can be adjusted from 4 and 5 to 2 and 3. Similarly, the values of *C. rutilus* would approximate 2 and 1, and those for *C. gapperi* 4 and 2. These estimates suggest weight loss values for these foods lower than those for ground lichens.

In summary, mushrooms far exceeded any other food in maintenance value, sustaining body weight with very little loss for as long as two months. Indeed, air-dried mushrooms were fed to the subjects regularly when it was found unnecessary to supply frozen fresh ones.

Cosmopolitan ground lichens, feather mosses and woody stems have the least maintenance potential. Arboreal lichens have possible value, their adjusted indices being lower than those for ground lichens, bryophytes, and possibly all other foods except mushrooms. The more succulent of the leaves and stems are of value but fruits are of little worth in maintenance



Table 13. Synopsis (mean  $\pm$  S.E.) of maintenance tests. Foods are categorized generally and arranged in increasing value to facilitate comparison; and adjusted for preference. Sample numbers are given in parentheses.

Category	Adjusted maintenance index (% initial weight loss/day)	
Fungi :		
<i>P. maniculatus</i>	1.9 ± 0.40	(4)
<i>C. rutilus</i>	1.3 ± 0.65	(4)
<i>C. gapperi</i>	2.6 ± 0.50	(4)
Arboreal lichens:		
<i>P. maniculatus</i>	2.5 ± 0.50	(2)*
<i>C. rutilus</i>	1.5 ± 0.50	(2)*
<i>C. gapperi</i>	3.0 ± 1.00	(2)*
Tracheophyte leaves:		
<i>P. maniculatus</i>	3.7 ± 1.13	(4)
<i>C. rutilus</i>	2.2 ± 0.29	(4)
<i>C. gapperi</i>	2.7 ± 0.62	(4)
Tracheophyte stems:		
<i>P. maniculatus</i>	4.7 ± 1.15	(2)
<i>C. rutilus</i>	3.1 ± 1.55	(2)
<i>C. gapperi</i>	2.8 ± 0.90	(2)
Tracheophyte fruits:		
<i>P. maniculatus</i>	4.3 ± 0.50	(7)
<i>C. rutilus</i>	3.8 ± 0.73	(7)
<i>C. gapperi</i>	5.1 ± 1.10	(7)
Ground lichens:		
<i>P. maniculatus</i>	5.8 ± 0.05	(2)
<i>C. rutilus</i>	4.3 ± 1.15	(2)
<i>C. gapperi</i>	8.5 ± 2.70	(2)
Bryophytes:		
<i>P. maniculatus</i>	5.4	(1)
<i>C. rutilus</i>	5.0	(1)
<i>C. gapperi</i>	8.7	(1)

\*Estimates (see text).



considering their high preference.

#### Rates of Water and Lab Chow Consumption

It is evident (Table 14) that the more diminutive *P. maniculatus* ate at a lower rate than either *C. rutilus* or *C. gapperi* ( $p < 0.001$ ). (This was also obvious while the subjects were being maintained on a diet of dry mushrooms. The mice ate approximately 2.5 grams per day; the voles, 4.0 grams per day.) *P. maniculatus* also ate less per unit body weight, although the difference was only significant when compared to *C. gapperi* ( $p < 0.05$ ). The difference in consumption of the two voles was not quite significant at the 5 per cent level.

When the data are divided by sexes, a higher rate per gram body weight is seen for the males of all three species. Although this difference is not significant statistically in any individual case, it exists in triplicate and is probably a real difference.

Measurements of water consumption (Table 15) show that, *in toto*, *P. maniculatus* drinks less than *C. rutilus* ( $p < 0.001$ ) and *C. gapperi* ( $p < 0.001$ ). This difference still exists when the values are divided by the respective body weights ( $p < 0.005$ ;  $p < 0.001$ ).

#### Natural Diet

Basic regimens. In the following discussion data from the stomach content analyses are presented for the four years synoptically. Assuming 4-year "oscillations" in the animals it is important that such a period is employed for these averages to insure representation of all phases of the fluctuation. The same period used for all three species makes





Table 14. Rates of consumption of laboratory food (mean  $\pm$  S.E.) provided *ad libitum* to non-breeding adults. Estimates are based on more than 25 days in each case. Sample numbers are given in parentheses.

Species and Sex	Grams per day	Grams per day per gram body weight
<i>P. maniculatus</i>		
Both sexes	2.53 $\pm$ 0.10 (24)	0.138 $\pm$ 0.006 (24)
Male	2.75 $\pm$ 0.12 (10)	0.148 $\pm$ 0.007 (10)
Female	2.43 $\pm$ 0.14 (14)	0.130 $\pm$ 0.008 (14)
<i>C. rutilus</i>		
Both sexes	3.50 $\pm$ 0.17 (15)	0.152 $\pm$ 0.006 (15)
Male	3.49 $\pm$ 0.23 (8)	0.157 $\pm$ 0.010 (8)
Female	3.50 $\pm$ 0.27 (7)	0.146 $\pm$ 0.007 (7)
<i>C. gapperi</i>		
Both sexes	3.71 $\pm$ 0.22 (20)	0.157 $\pm$ 0.008 (20)
Male	3.64 $\pm$ 0.40 (10)	0.159 $\pm$ 0.012 (10)
Female	3.78 $\pm$ 0.21 (10)	0.155 $\pm$ 0.011 (10)



Table 15. Rates of voluntary water intake (mean  $\pm$  S.E.) by some of the subjects. Estimates are based on more than 25 days in each case. Sample numbers are given in parentheses.

Species	cc/day	cc/g body weight/day
<i>P. maniculatus</i>	5.55 $\pm$ 0.49 (17)	0.30 $\pm$ 0.29 (17)
<i>C. rutilus</i>	10.87 $\pm$ 0.89 (8)	0.47 $\pm$ 0.04 (8)
<i>C. gapperi</i>	13.43 $\pm$ 1.70 (12)	0.58 $\pm$ 0.07 (12)



comparisons meaningful. Data are discussed in terms of *relative volume*, *absolute volume* and *frequency of occurrence*.

*Relative volume.* The overall consumption spectra expressed as aggregate percentages by volume of total stomach contents are given in Appendix V. Figure 29 is a free-hand construction of these spectra with the lines smoothed for ease of presentation and interpretation. Note that the graph fails to show some foods eaten exiguously and, therefore, suffers a loss of detail. The diets of the two species of *Clethrionomys* are represented throughout the twelve-month period, but stomachs of *P. maniculatus* were not taken during the winter when they were almost impossible to catch (Stebbins, 1968; Fuller, Stebbins and Dyke, 1969). There is also a paucity of voles for the long winter period when few workers were in the field. For convenience the regimens of the two rodent genera are discussed separately below.

During the spring months of April, May and most of June, *P. maniculatus* ate progressively greater proportions of arthropods, mostly insects (see Fig. 17), supposedly as these became increasingly more available, until by the end of June they almost comprised the entire diet. At the end of June insect eggs appeared. Feathers occurred occasionally.

For the first part of the spring period very small amounts of achlorophyllous vegetative material was consumed. It is not known how much of this component was root material which, projecting from central Alberta collections, was expected in much larger proportions (W.H. Sharp, *pers. comm.*). Unless root material also formed a part of the unidentified portion of the diet, it is of little importance and fossorial food collecting cannot be assumed. Any stem material from this portion of the diet probably comes from the more highly-preferred succulent species (Figs. 24, 25 and 27).

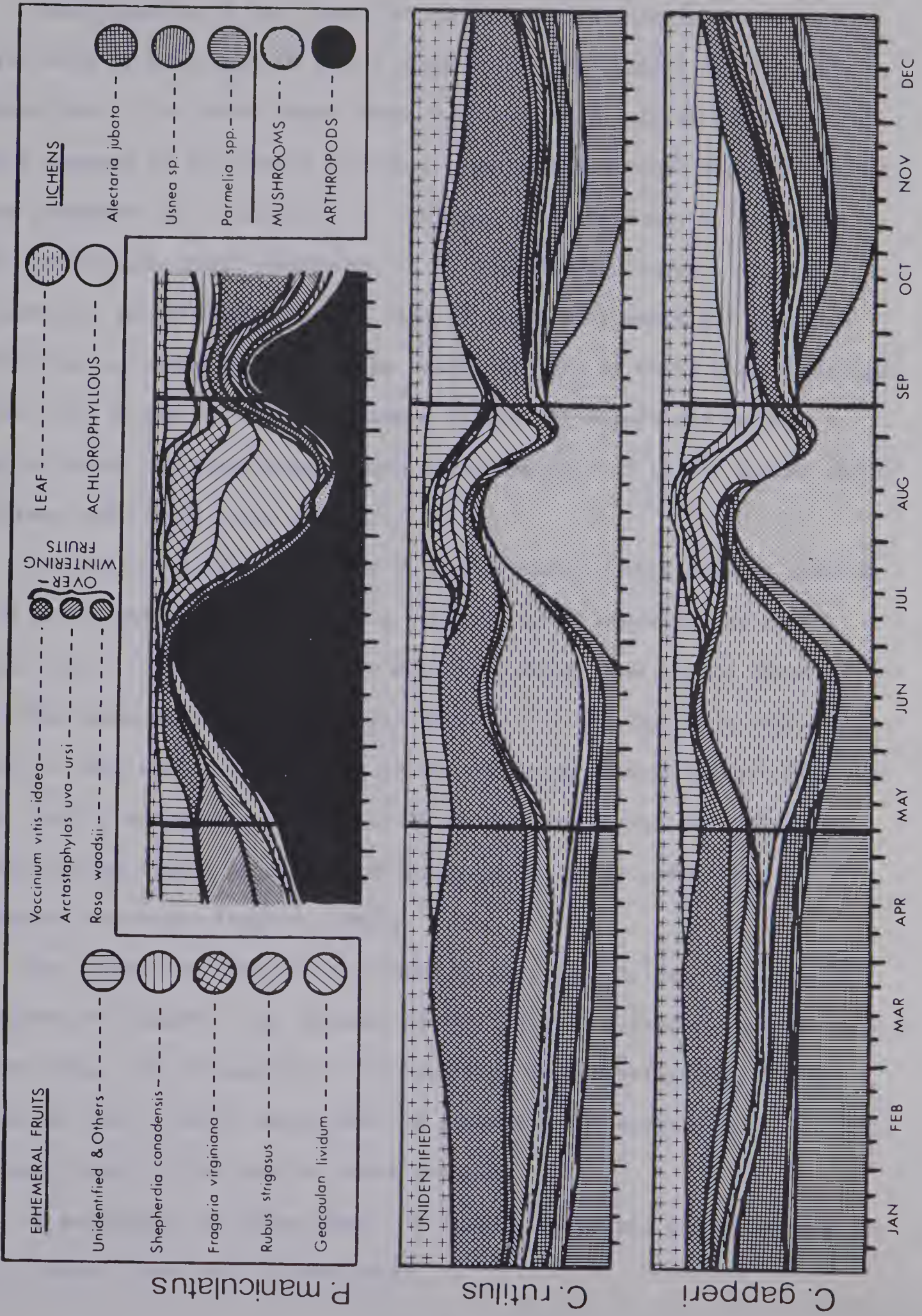






Figure 29. Basic dietary regimens of the three rodents averaged for four years and expressed as percentage volume. Raw data and sample numbers are given in Appendix V. The vertical lines bound the period expanded in Figure 31.

Percentage by volume







Small amounts of leaf material, especially obvious in May and the first half of June, were of little quantitative importance in the early summer diet. Its constituents were "needles" of *E. nigrum* and *Picea* spp.; trace amounts of *Hylocomium splendens* (and possibly other feather mosses); leaf fragments of *A. uva-ursi*, *G. lividum*, *F. virginiana*, *L. borealis*; and surprisingly small quantities of *P. tremuloides* leaves. It was suspected *a priori* that, at this time of year, mice would eat greater quantities of young *P. tremuloides* leaves because of their high preference (Figs. 24, 25 and 27) and maintenance (Table 12) values and because a single animal had been trapped with a half-eaten leaf in its buccal cavity (Friesen and Floyd, *pers. comm.*).

The remainder of the diet of *P. maniculatus* in this season, outside of a little unidentified material, was made up of overwintered fruits, mainly those of *R. woodsii* and *A. uva-ursi*, which gave way to those of *V. vitis-idaea* during mid-May. The fruits of *R. woodsii* were probably eaten in such substantial ratios in the prevernal period because they are more readily accessible while snow is on the ground than the other two overwintering fruits which are low-growing. *R. woodsii* may also be important in winter (Fuller, 1969b).

The unknown portion of the fruits at this time is not likely to be composed of *Juniperus* spp. because of the latter's extremely low preference values (Figs. 24, 25 and 27). The remaining two overwintering fruits, *V. oxycoccus* and *R. rubra*, which were of extremely low availability (Appendix IV) were found in the diet in trace amounts.

If vegetative or floral buds, or flowers augmented the mouse diet in early summer, they were unidentified.





Throughout the remainder of the summer (July and August), as ephemeral fruits became available, insect consumption dropped off concomitantly. Fruits of *S. canadensis* were first to appear in the environment (Appendix III) and in stomachs, though at that time (late June) those fruits were rare and inaccessible because of the height of the shrubs and because the fruits had not yet dropped off and were, consequently, eaten in only small amounts. In order of fructification, green fruits of *F. virginiana* appeared next in mouse stomachs, followed by green *G. lividum* berries, and finally those of *R. strigosus* (Appendix III). During the fruiting season *G. lividum* fruits were consumed extensively, followed in order of importance by those of *R. strigosus*, *F. virginiana* and *S. canadensis*. On three occasions in 1966, 9, 2 and 7 fruits of *G. lividum* were found in the buccal cavity of *P. maniculatus*. These consisted mainly of seeds, the flesh having been swallowed. From these observations, and the lack of seed coat fragments in stomach contents, it is speculated that only flesh of this fruit is eaten (see also Appendix II). The low consumption of *S. canadensis* berries is explainable either by preference (Figs. 24, 25 and 27) or availability (Fig. 22; Tables 4-7 and Appendix IV). Judging from the preference studies one would expect *R. strigosus* fruits to be consumed by deermice in much greater quantities than the fruits of *F. virginiana*. The fact that they were consumed equally as much (Fig. 29) must be a result of the much greater accessibility of the latter which forms a part of the ground cover, as opposed to the former whose fruits are borne high on thorny stems. In addition, *F. virginiana* fruits were more plentiful than those of *R. strigosus* in the forest environments with which this survey is concerned (Appendix IV). These are probably the same reasons why the low-growing, very plentiful *G. lividum* fruits were also eaten more



than the more highly preferred fruits of *R. strigosus*. Indeed, the lag between the beginning of fruiting of *R. strigosus* (Appendix III) and its consumption (Fig. 29) is likely the time necessary for the ripe fruits to begin dropping to the ground. Why the fruits of *G. lividum* were eaten more than those of *F. virginiana* may be a matter of preference (Figs. 24, 25 and 27) or availability (Appendix IV), accessibility being apparently equal.

Mushrooms could not be identified as to type, but judging from the preference (Figs. 24, 25 and 27) and availability (p. 63) results, *Russula* is most likely to have occurred among the stomach contents. That this food comprised such a scanty proportion of the diet of *P. maniculatus* is unexplainable considering its preference, availability and nutritional worth (Tables 12 and 13). Were it not for equal preference the simultaneous occurrence of fruits in the environment would explain this phenomenon.

At that time, too, overwintering berries were being replaced in the diets of the animals by their fresh counterparts. In the laboratory these fresh berries were preferred to overwintered ones by *P. maniculatus* (Fig. 26), but this preference was not reflected in consumption because, as long as the ephemeral types were available, the overwintered ones made up little of the diet. This must have been a manifestation of preference (Figs. 24, 25 and 27) because accessibility and availability of the overwintered fruits were as good as, if not better than, those of the ephemeral ones. The high preference for *A. uva-ursi* berries, though, was not borne out in the consumption data of that season.

In September, as ephemeral fruits became scarce, insects again made up a substantial proportion of the deermouse diet, and overwintering fruits assumed their former importance. The exclusion in August of insects





and overwintering fruits by ephemeral fruits attests to the animals' higher preference for the latter (see also Figs. 24, 25 and 27). By late October the insect content of the diet had again dropped off almost completely, this time likely as a result of diminishing availability.

At the same time achlorophyllous parts and green material (mainly leaves of *S. canadensis* with traces of leaves of *A. uva-ursi*, *L. borealis* and *P. tremuloides*; and *H. splendens* and possibly other feather mosses) reappeared, but contributed little volume.

Among the overwintering fruits, those of *V. vitis-idaea* became more and more prominent in the mouse diet as the fall progressed and, in October, were eaten five times more than the others. As in the fruiting season, the high fall preference (Fig. 26) for *A. uva-ursi* berries and their low consumption is inexplicable considering their overall availability (Appendix IV), unless due to habitat shift (Fig. 36).

Of the ephemeral fruits, *S. canadensis* berries were eaten well into the fall in greater amounts than in the previous period. This is probably because they were dropping to the ground in great numbers at that time (a characteristic of the species), and because the more highly preferred ephemeral fruits (Figs. 24, 25 and 27) were no longer available, save for a few of *R. strigosus*. Traces of the fruits of *R. oxyacanthoides*, *R. acaulis*, *M. nuda*, *A. uva-ursi* and *A. polifolia* were also found in the stomachs at that time. Although the fruits of *R. oxyacanthoides* are highly preferred (Figs. 24, 25 and 27), they were probably relatively inaccessible because of their location on tall thorny shrubs, and restriction to only a few biotopes. As for the other fruits, preference and availability alone easily explain consumption results.

One can only speculate on the contents of the "unidentified" fruit





category which became prominent in the mouse diet in late August. Seeds larger than 2 mm were not found whole in the stomachs (Fig. 17) so this portion could contain the seeds of spruce (*Picea* spp.) or of *C. stolonifera*, both of which should be common in the area and which are too large to ingest in diagnostic proportions; or, similarly, those of the highly preferred *V. edule* (Figs. 22-24 and 26). *E. nigrum* berries were suspected *a priori* to form part of the diet, but since their seeds are too small to be totally pulverized and can be recognized microscopically, that species certainly did not contribute to the diet. The small diagnostic seeds of overwintering *V. oxycoccus* were not found either, probably because that species was so scarce. *Juniperus* berries, especially the pericarp (p. 76), although ruled out in the spring period (see above) may be important (Fig. 26), particularly when their numbers in the environment are taken into account.

The winter diet of *P. maniculatus* may be extrapolated from the data of Figure 29 and from environmental availability to consist of achlorophyllous and green material and the three overwintering fruits. Insects, lichens and ephemeral fruits are probably unimportant contributors to the diet at that time.

The diet of *Clethrionomys* spp. differed in many ways from that of *P. maniculatus*. The most obvious feature of the vole spring regimen is that they did not eat insects, but ate great quantities of green material. The volume of green material increased throughout May and the first half of June when spring foliage reached full development in the environment (Appendix III), and decreased until it disappeared altogether at the end of July. The chlorophyllous content consisted of *S. canadensis* leaves; *H. splendens* (also other feather mosses); leaves of *P. tremuloides* and *A.*



*uva-ursi*; and much unidentified material.

Only a trace of achlorophyllous parts was eaten in spring but, in contrast to the diet of *P. maniculatus*, substantial quantities of arboreal lichens were ingested in decreasing magnitude up to the fruiting season. Since these lichens are found on detached branches lying on the ground, as well as on standing trees, it is not necessary for the voles to climb to reach them. The arboreal lichens consisted of *Alectoria jubata* and *Parmelia* spp. in equal proportions in the *C. rutilus* diet, but weighted in favor of the latter in the diet of *C. gapperi*. *A. jubata* is a fine, dark, inconspicuous threadlike lichen (Fig. 17 and Appendix II) which is very rare and must be extricated from tree bark and the undersides of *Parmelia*. This species must have been assiduously sought out in order to have been eaten in such large quantities relative to the conspicuous and plentiful *Parmelia* species. This is especially true where *C. rutilus* is concerned.

Of the three overwintered fruits in the spring diet, *R. woodsii* (probably mainly pericarp—Table 10) made up a very small proportion after the snow disappeared. This proportion probably more truly reflected the low preference of *Clethrionomys* for that fruit than did the winter diet when necessity may have dictated its consumption. The fruits of *A. uva-ursi* and *V. vitis-idaea* seemed to be eaten according to spring preferences (Fig. 26) since these were roughly equally available and accessible during that period. It is notable that *V. vitis-idaea* berries, the most highly preferred of overwintering fruits, made up the bulk of the fruit diet (six times more than the others) in *C. rutilus*, causing a slight decrease in consumption of green material and *Parmelia* spp. in that species as compared with *C. gapperi*. This was likely due to greater availability of





*V. vitis-idaea* fruits in *C. rutilus* territory (compare Tables 6 and 7).

In spring the "unknown fruit" category of the *Clethrionomys* diet likely did not include *Juniperus* berries (Fig. 26). However, *A. uva-ursi* berries (Fig. 17 and Appendix II), the tiny granules of which are not as microscopically obvious in the more finely masticated contents of *Clethrionomys*, may have contributed.

During the fruiting season mushrooms appeared in the environment and in the vole diets at the same time as did the ephemeral fruits, and together they progressively replaced chlorophyllous parts, arboreal lichens and, to a great extent, overwintered fruits. Mushrooms became the primary food (around 65%) in early August in both species of *Clethrionomys*. According to preference (Figs. 24, 25 and 27), and observations of availability and feeding evidence (teeth marks and feces) in the environment, this part of the diet consisted mainly of *Russula* sp.

Ephemeral fruits appeared in the vole stomachs according to their phenological accession and attained the same relative importance as in mice; but, with the exception of *S. canadensis* berries, voles ate less fruit than did mice. A lower preference of voles than mice for *G. lividum* and *R. strigosus* berries (Figs. 24, 25 and 27) may reasonably explain the relative lack of these seemingly equally obtainable foods in the vole stomachs. But the more highly preferred *F. virginiana* fruits (Figs. 24, 25 and 27), also presumably equally accessible to both genera, were eaten in lesser quantities by *Clethrionomys*. The simultaneous advent of the mushroom crop may partly explain this low consumption, although the preference studies do not substantiate it. Annual comparisons (see next section),





however, showed that the mushroom fraction of the diet replaced the fruit content in the "mushroom years." The *relative* quantities of these fruits may be explained by preference, except in the case of *G. lividum* where availability was believed to be important. The overwintering fruits have low preference values (Figs. 24, 25 and 27), especially in the fruiting season (Fig. 26) and, as in *Peromyscus*, the newly-formed fruits were eaten in much smaller amounts than their overwintered counterparts in the spring.

Mushrooms comprised a decreasingly small proportion of the autumn diet, and were not eaten at all after the end of October. During that period ephemeral fruits appeared which were of secondary importance to the diet as a whole. Among these were the little-preferred fruits of *R. oxyacanthoides* and some of *C. canadensis* and *C. stolonifera*. The latter, though not recognizable in the stomach, were found in the buccal cavity of *C. gapperi*. The berries of *R. chamaemorus* were eaten by this genus in the muskegs which habitat they shared to a very large extent with *P. maniculatus*. *V. edule* fruits are probably also among the unidentified portion (Figs. 24, 25 and 27).

Generally, the disappearance of ephemeral fruits from the diet coincided with the first snowfall in early October, but *S. canadensis* berries increased in quantity in the stomachs of *C. gapperi* until the end of November. It is assumed that, because these fruits had dropped off the shrubs by that time, their increased consumption can be explained by availability.

*C. rutilus*, on the other hand, ate fresh *V. vitis-idaea* berries in increasing quantities after the fruiting season until these made up almost half the total diet, whereas only about one-third as many were eaten by



*C. gapperi*. Less preferred (Figs. 24, 25 and 27) *S. canadensis* fruits take the place, in *C. gapperi*, of the less available (Tables 6 and 7, and Appendix IV) *V. vitis-idaea* in *C. rutilus*.

Achlorophyllous parts, probably containing bark according to laboratory observations, and green material, including leaves of *P. tremuloides*, *E. nigrum* and feather mosses, were again eaten in small amounts in the fall; and the overwintering fruits of *A. uva-ursi* and *R. woodsii* appeared in the diets for the duration of the winter.

In mid-September, arboreal lichens became part of the diet, and increased in importance during the first half of the winter. Of these, *Parmelia* spp. came to make up about one-third of the total diet of *C. gapperi* and one-quarter of that of *C. rutilus*. *Alectoria jubata* which, judging from the spring diet, was of greater importance to *C. rutilus*, was eaten in much greater quantities in winter by *C. gapperi* (four times as much). *Usnea* sp. was taken in small amounts by both species. The lower intake of arboreal lichens by *C. rutilus* can be explained by its higher winter consumption of *V. vitis-idaea* berries and this, in turn, by availability.

The percentage of unidentified material increased in vole diets during winter months. Preference studies (Table 11) suggest that the prevalent ground lichens, especially *Cladonia* spp., may have been eaten in winter; though, unfortunately, this material could not be identified in the stomachs. Further substantiation came on November 13, 1965 when L.L. Stebbins (*pers. comm.*) took a specimen of *C. rutilus* with its buccal cavity crammed with *Cladonia* spp.

Monocot leaves (including graminoids, scanty in the area) were noticeably absent from the stomach contents of both *Clethrionomys*



and *Peromyscus*. Their absence must be a matter of preference (Figs. 24, 25 and 27) and not availability or accessibility (Appendix IV). Another notable exclusion is tree seeds which are either not eaten at all, or the small, potentially diagnostic seeds are not eaten whole and the seed content comprises a part of the "unidentified" portion.

*Absolute volume.* Figure 30 shows absolute measurements of the stomach contents of all three animals by sex and age. All the data from juveniles of *Clethrionomys* spp. are grouped into August (since it is the month when the majority were taken) to avoid attenuation of scanty data. The large number of juveniles of *P. maniculatus* are not so aggregated. Since no sexual differences were found to exist in data from the young, males and females are pooled.

It is immediately obvious that, if volume indicates rate, the mice did not eat perceptibly less food than the voles, notwithstanding laboratory observations (Table 14).

Juvenile animals, which masticated their food more finely, had smaller volumes of stomach contents than the adults (only significant if compared to adults of all months together). Younger animals differed only in their lower consumption of ephemeral fruits.

Females had larger stomach contents than males, perhaps a reflection of unequal quantitative requirements for reproduction. The difference is especially striking in May (significant in all three species), which is a time of rapid weight gain in females (Fuller, Stebbins and Dyke, 1969). During winter males had larger ( $p < 0.05$ ) stomachs than females, as did non-reproductive males in the laboratory (Table 14).

The increased bulk of the female vole stomachs in May is mainly attributable to greater consumption of arboreal lichens and, to a lesser

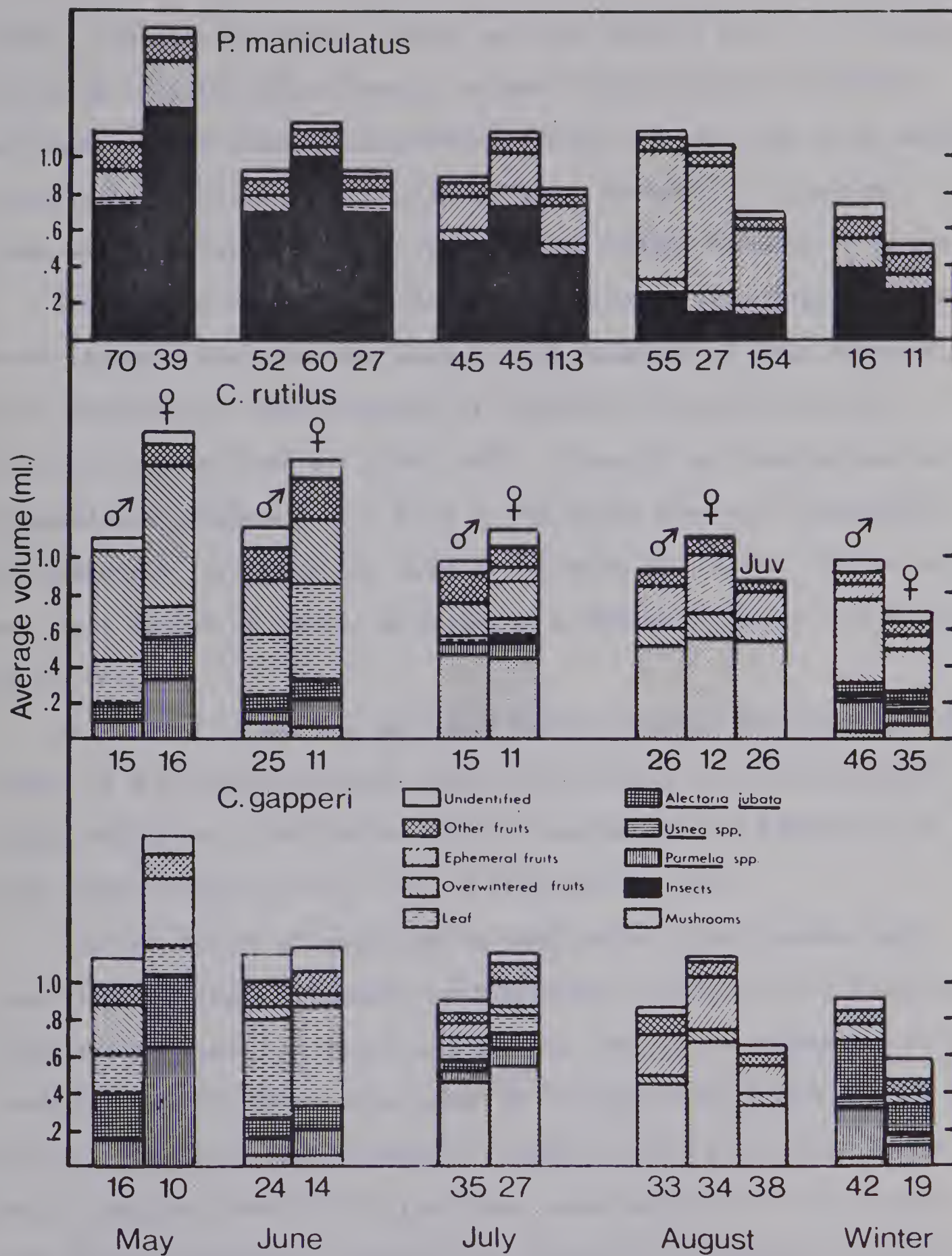








Figure 30. Absolute volumes of the examined stomach contents arranged by sex and maturity. For convenience, the fruits are combined into two categories, since they showed no particular sexual or chronological trophic associations. The sample number is given below each bar graph.





degree, overwintered fruits. Leaves may have played a role in *C. rutilus*. During the fruiting season females consumed slightly greater volumes of mushrooms and overwintered and ephemeral fruits. In the mice these sexual differences are totally explainable by insect consumption. The same foods were responsible for the greater volume of male stomachs in winter.

*Frequency of occurrence.* The data expressed as percentage of occurrence (Appendix VII) show few cases of high frequency of foods eaten in small amounts as is characteristic of incidental ingestion of widely-distributed foods (Ward and Keith, 1962). Examples were feather moss which occurred more frequently ( $p < 0.01$ ) in the winter diet of *P. maniculatus* and arthropods, *A. jubata* and *Usnea* sp. in voles ( $p < 0.05$ ). Female voles ate trace amounts of insects in spring at a greater frequency than males ( $p < 0.001$ ).

Boli of hair, probably swallowed during grooming, were more ( $p < 0.001$ ) common in the spring and winter periods than during the fruiting season and, except during the winter period when it occurred equally frequently, of more common occurrence ( $p < 0.05$ ) in mice than in voles.

The frequencies of appearance of sand grains in the stomachs were ascertained in order to examine the hypothesis of Horner *et al.* (1965) who suggested that sand may abrade soft tissues from chitin fragments. Of the stomachs in which insects were found, 29 contained sand grains and 318 did not. Of stomachs without insects, 11 contained sand grains and 356 did not. Therefore, there is no significant association ( $\chi^2 = 1.1$ ) of sand with insect consumption, implying that ingestion is accidental in spite of a higher incidence ( $p < 0.001$ ) in spring when insects are eaten.

Nematodes of various sizes were sometimes found in the stomachs of adult voles but never in juveniles or mice of any age. They were found







unmasticated, usually one or two at a time; but one female *C. rutilus* caught in June contained nine. The only winter incidence was that of three individuals found in a *C. gapperi* stomach.

Throughout the year and in all species, sexes and ages, red threads of the ribbons of trap markers, as well as peanut butter, occurred occasionally in the stomachs.

The trophic fundamentals may now be summarized as follows:

1) Seasonally, food habits reflected the compressed and compartmentalized phenology, manifesting the general influence of availability. Otherwise, preference appears to have dictated consumption patterns.

2) Oligophagic diets during the fruiting season, and opportunism at other times, characterized both genera.

3) Frugivory was shared by both genera (to the same extent in years when mushrooms were not available), a fact not predicted through morphological studies. Overwintering fruits were important when other fruits were not in season, supplemented by insects in *Peromyscus* and by vegetative parts and mushrooms in *Clethrionomys*. Herein lay the trophic difference of these genera. As predicted, the two species of *Clethrionomys* had similar diets.

Annual comparisons. The data from the stomach content analyses are now analyzed by year and presented as *relative volume*, *absolute volume* and *frequency of occurrence*.

*Relative volume.* The intervals bounded by the heavy vertical lines drawn at early May and early September (Fig. 29) are expanded to cover the four years in Figure 31. Lines are smoothed from the values of Appendix VI for visual convenience but, unfortunately, because of lack of uniformity





Figure 31. Summer dietary regimens by percentage volume of the three rodents expanded over the four years of the study. Raw data and sample numbers are given in Appendix VI. The legend is given in Figure 29.



A black and white woodcut illustration of a stylized, abstract figure, possibly a woman, with a large, rounded head and a long, flowing, patterned garment. The figure is set against a dark background with a vertical ruler-like scale on the left side.

MAY JUN JUL AUG SEP

A stylized, high-contrast illustration of a person's profile, rendered in black and white with a halftone dot pattern. The image is framed by a thick black border. The profile is facing right, with the head tilted slightly upwards. The hair is short and dark. The neck and shoulder area are visible, with the shoulder having a distinct, textured pattern. The background is a light gray with a fine halftone dot pattern. The overall style is graphic and minimalist.

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in the temporal distribution of the data (Tables 2 and 3), extrapolation and speculation were sometimes necessary. This was especially true for 1967 when 100 stomachs were lost, and for 1968 when population numbers were low (see sample numbers in Appendix VI).

The spring diet of *P. maniculatus* consisted essentially of overwintered fruits and arthropods. Although overwintered fruits were most abundant on the study area in 1967 (Fig. 22), arthropods were consumed in greater proportions that spring than in any other ( $p < 0.005$  for increase over previous year) and in late June amounted to monophagy. Whether this was due to a possible higher preference (Figs. 24, 25 and 27) or greater availability is not clear.

Despite the yearly variations in fruit crops (Fig. 22) *P. maniculatus* consumed the same total proportion of fruits in late summer every year. Only the time of appearance in the diet (reflecting phenological advent) and the relative abundance of species (reflecting availability) changed. Thus, in 1966, when they were most available, *G. lividum* fruits made up one-half of the diet, but in the poor "fruit year" of 1967 the mouse diet did not shift to other foods but made up for the lack with less-preferred *S. canadensis* fruits and overwintering ones, many of which had survived from the large crop of the year before. In 1968 relatively highly available (Fig. 22) fruits of *F. virginiana* and traces of those of *R. oxyacanthoides* made up the deficit.

Yearly variations also took place in the *Clethrionomys* spring diet of overwintered fruits, new leaves and arboreal lichens. The plentiful overwintered fruits in 1967 (Fig. 22), especially the highly preferred (Figs. 24, 25 and 27) *V. vitis-idaea* fruits which almost monopolized the stomach contents of *C. rutilus*, replaced leaf material and arboreal lichens



in the diets. The poor overwintered fruit supply in the spring of 1968 was again augmented in the vole diets by leaves and arboreal lichens.

*Clethrionomys* diets of late summer were composed of ephemeral fruits (especially *G. lividum*) in years when they were available and mushrooms were not (1965, 1966), and of mushrooms (with little recourse to overwintering fruits) when they were available and fruits were not (1967, 1968) ( $p < 0.05$ ). That the voles managed to glean and consume the very scarce mushrooms to the magnitude of one-third of their diet in 1965 and 1966 indicates the major role of preference in the ingestion of that food.

Figure 32 presents the percentage by volume of the winter stomachs of *Clethrionomys* taken in 1965-66 and 1966-67. These data are grouped into single bar graphs because of the little variation throughout the winter in the various elements of the diet (see Fig. 29).

The major difference between the two winters is in the higher proportionate consumption of *V. vitis-idaea* fruits in the winter of 1966-67 at the expense of the arboreal lichen portion ( $p < 0.05$ ). This difference is especially prominent in *C. rutilus*.

Besides the prevernal and late fall specimens (Fig. 29), only three winter stomachs of *P. maniculatus* were taken—two in January and one in February of 1966-67. These were filled with overwintering berries, mainly of *R. woodsii*. At that time piles of *R. woodsii* seeds and their cracked testae were evident near the roadside by the parklike jackpine stand in *C. gapperi* territory where these fruits abounded.

*Absolute volume.* Absolute volumes of total stomach contents are given in Table 16. To strengthen averages, autumn and prevernal values are grouped into the vernal and fruiting periods rather than winter, and the latter period is represented only by *Clethrionomys* spp. for 1965-66





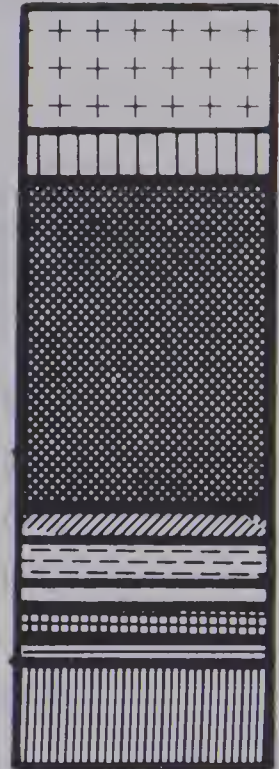
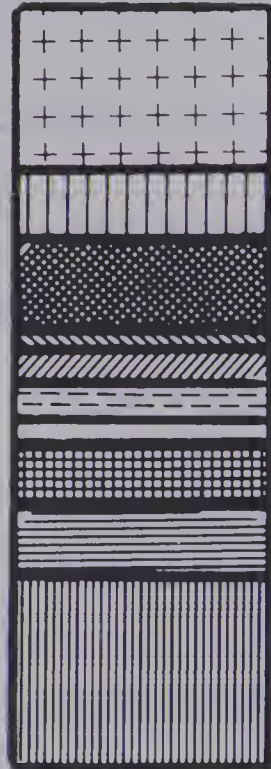
Figure 32. Percentage composition of the winter stomach contents of the two species of *Clethrionomys* taken in 1965-66 and 1966-67. The sample number is given above each bar graph. The legend is given in Figure 29.



45

28

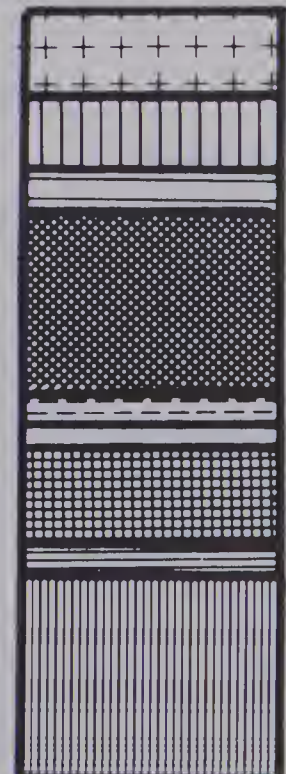
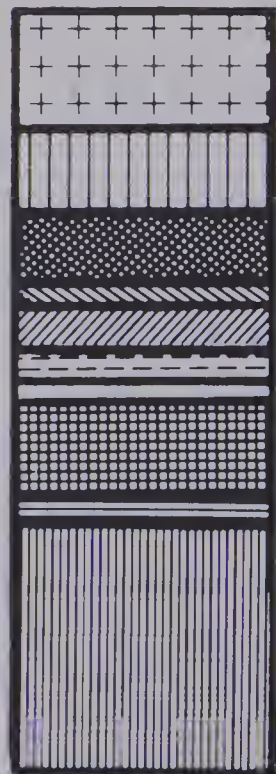
C. rutilus



30

22

C. gapperi



1965 - 66

1966 - 67



Table 16. Volumetric measurements (mean  $\pm$  S.E.) of the total stomach contents by year and season. The sample numbers are given in parentheses.

Species	Time	Volume (ml)		
		Vernal Period	Fruiting Season	Winter
<i>P. maniculatus</i>	1965	1.10 $\pm$ 0.14(98)	0.86 $\pm$ 0.12(96)	
	1966	0.94 $\pm$ 0.14(32)	0.81 $\pm$ 0.05(217)	
	1967	1.28 $\pm$ 0.16(68)	1.10 $\pm$ 0.08(67)	
	1968	1.21 $\pm$ 0.18(53)	0.94 $\pm$ 0.08(81)	
<i>C. rutilus</i>	1965	1.42 $\pm$ 0.24(28)	0.94 $\pm$ 0.27(23)	
	1965-66			0.95 $\pm$ 0.06(50)
	1966	0.78 $\pm$ 0.15(14)	1.50 $\pm$ 0.37(19)	
	1966-67			1.58 $\pm$ 0.28(31)
	1967	1.53 $\pm$ 0.32(20)	0.71 $\pm$ 0.16(22)	
	1968	1.51 $\pm$ 0.40(11)	0.86 $\pm$ 0.14(20)	
<i>C. gapperi</i>	1965	1.60 $\pm$ 0.72 (6)	1.01 $\pm$ 0.23(11)	
	1965-66			0.93 $\pm$ 0.14(35)
	1966	1.16 $\pm$ 0.31(19)	0.94 $\pm$ 0.09(116)	
	1966-67			1.12 $\pm$ 0.22(26)
	1967	1.27 $\pm$ 0.18(29)	1.02 $\pm$ 0.31(13)	
	1968	1.64 $\pm$ 0.42(17)	0.95 $\pm$ 0.15(21)	



and 1966-67.

Simultaneous consideration of Figure 31 and Table 16 suggests that the drop of spring insect content in the *P. maniculatus* diet in 1965-66 occurred *absolutely* ( $p < 0.02$ ) as did the 1966-67 increase ( $p < 0.025$ ) and the 1967-68 decrease ( $p < 0.05$ ). Total amounts of overwintered fruits in the vernal period and ephemeral fruits in late summer remained constant in an absolute sense.

In *Clethrionomys*, a drop in total volume occurred in the spring of 1966 ( $p < 0.05$  for *C. rutilus*; not significant for *C. gapperi*) (Table 16). An increase again in 1967 ( $p < 0.05$  for *C. rutilus*; not quite significant for *C. gapperi*) was mainly caused by greater absolute volumes of overwintered fruits, mainly those of *V. vitis-idaea* ( $p < 0.02$  for both voles). In the fruiting season 1966 stomach contents were greater in *C. rutilus* than in *C. gapperi* ( $p < 0.05$ ), the bulk of which difference was mushroom.

The absolute volume of stomachs (Table 16) was greater in the winter of 1966-67 than in 1965-66, but significantly so ( $p < 0.02$ ) only for *C. rutilus*. A simultaneous consideration of Figure 32 reveals that this increase was due to *V. vitis-idaea* fruit alone, with *S. canadensis* berries contributing minimally in *C. gapperi* in the late fall.

*Frequency of occurrence.* In terms of frequency of ingestion there was no evidence of increased foraging activity by *P. maniculatus* in poor periods. However, *Clethrionomys* ate feather moss more frequently ( $p < 0.005$  for *C. rutilus*;  $p < 0.05$  for *C. gapperi*) in the spring of 1968 than in that of 1967 and *Parmelia* at a lower rate ( $p < 0.001$  for *C. gapperi*) in the spring of 1967 than in 1966. The consumption data are expressed as percentage occurrence in Appendix VIII.

Miscellaneous items showed no year-to-year peculiarities, with the







exception of the nematodes which were not found in 1967.

In summary, annual consumption differences reflected availability to some extent. The phenological occurrences reflected in the stomach contents were:

- 1) the lags of 1967 and 1968;
- 2) the "fruit year" of 1966 and the poor fruit production of 1967;
- 3) the good overwintering berry crop of 1966, and the poor one of 1967;
- 4) the high mushroom crop of 1967, followed in magnitude by that of 1968.

The tendency for good fruit years to be poor mushroom years and vice-versa is not a danger to voles which may switch from one of these foods to the other. On the other hand, deermice eat little mushroom, notwithstanding laboratory preferences (Figs. 24, 25 and 27) and have only less-preferred (mostly overwintering) fruits to fall back on. The higher preferences of *P. maniculatus* for fresh fruits in fall than their overwintered counterparts in spring (Fig. 26) is now clear. The opposite situation was seen (Fig. 26) for *C. gapperi*. Generally, the trophic situation is potentially more precarious in late summer for mice than for voles because mice do not switch diets.

Biotopic comparisons. The compositions of the stomach contents are shown in Figures 33, 34 and 35. The data, divided by biotope, allow seasonal deployment into three categories—"vernal," "fruiting," and "winter" periods as in Table 16. Only the "mixed forest" habitat provided enough stomachs to display a seasonal continuum but, for comparative reasons, it is treated in the same way as the rest.





Figure 33. Dietary make-up by absolute stomach volume of *P. maniculatus* averaged by biotope for the years 1965-68 inclusive. The sample number and reason for omission are given in each case. The legend is given in Figure 29.

# Vernal Period

# Fruiting Period

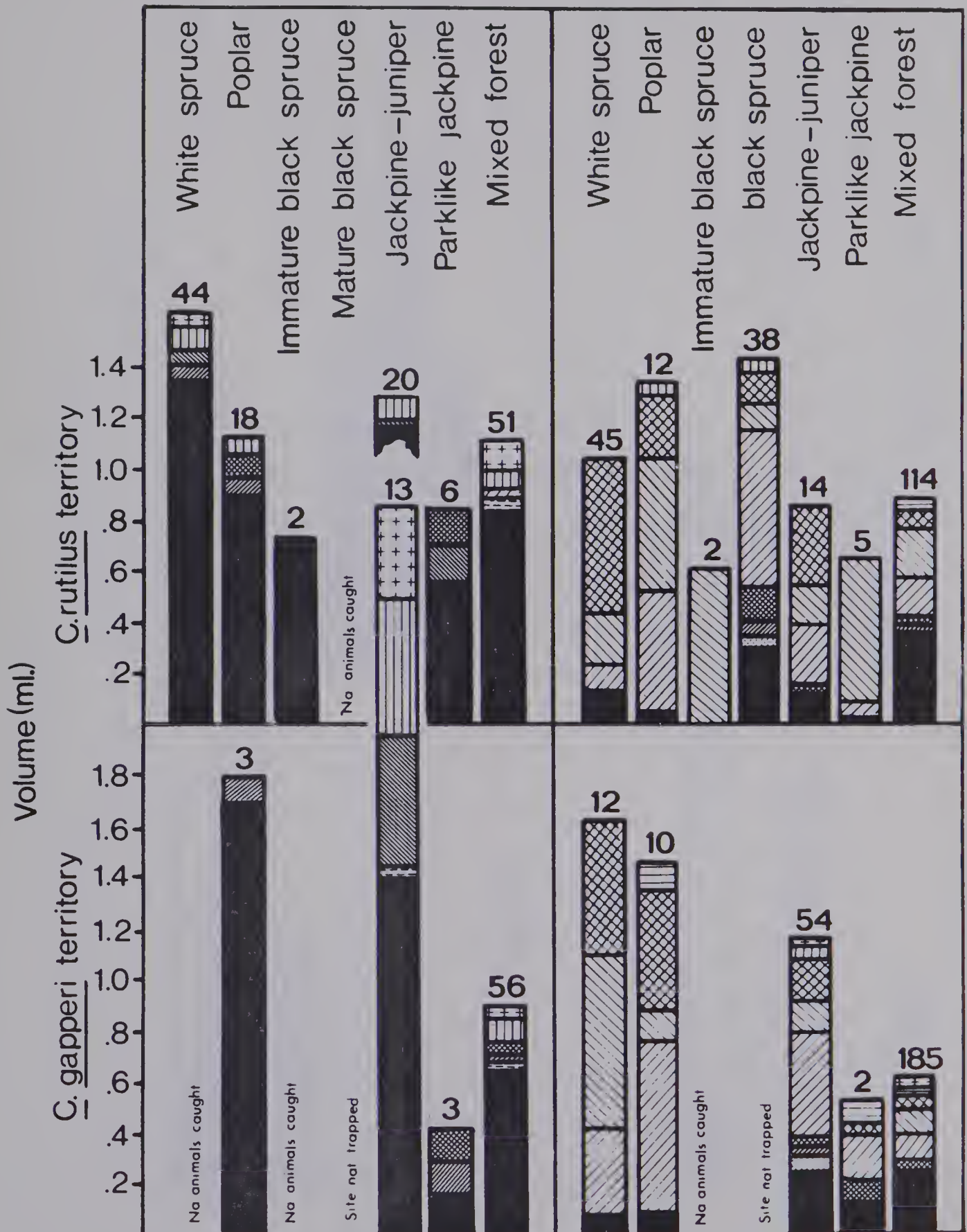








Figure 34. Dietary make-up by absolute stomach volume of *Clethrionomys* spp. averaged by biotope for the years 1965-68 inclusive. The sample number and reason for omission are given in each case. The legend is given in Figure 29.

# Vernal Period

# Fruiting Period

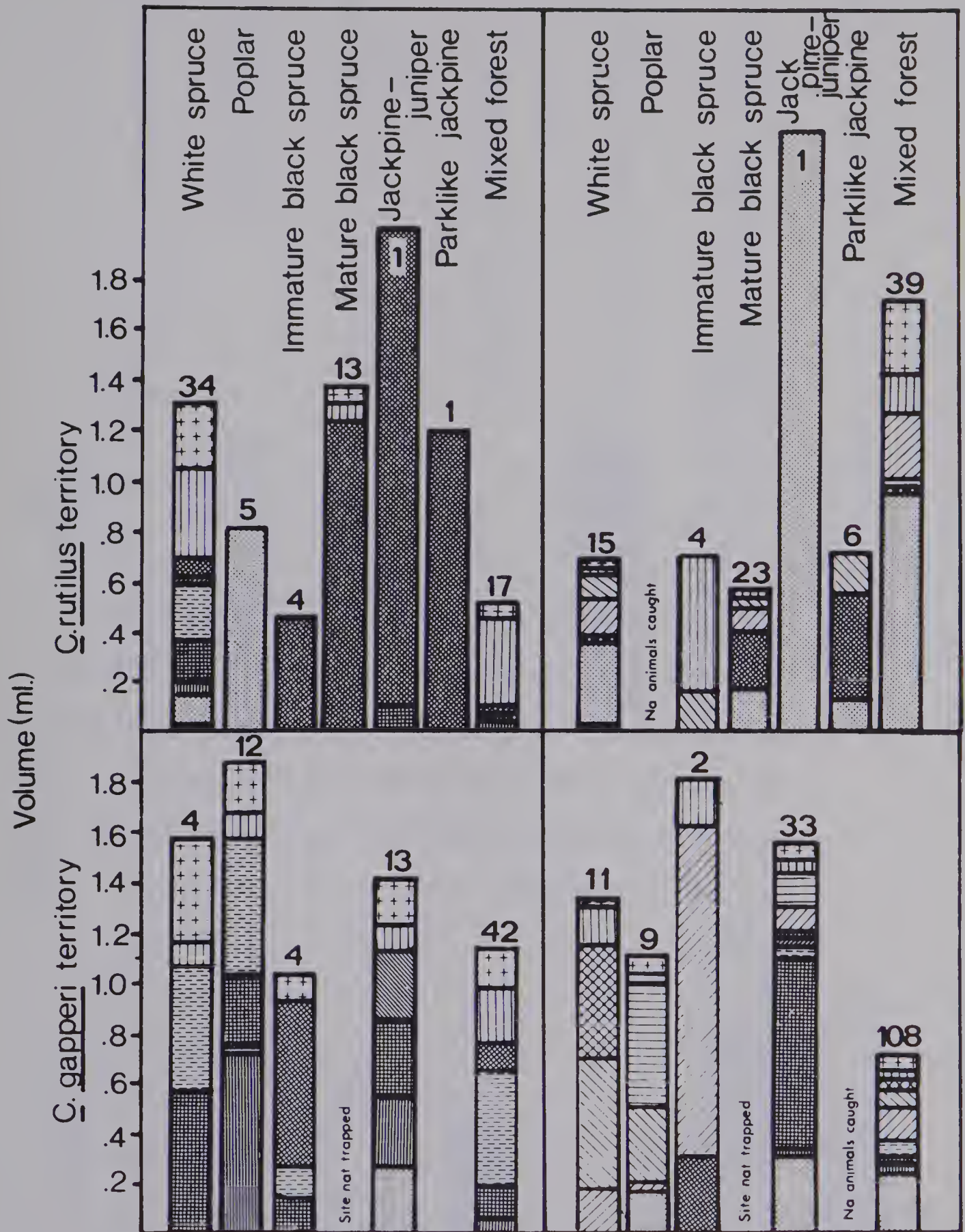






Figure 35. Winter dietary make-up by absolute stomach volume of *Clethrionomys* spp. averaged by biotope for the 1965-66 and 1966-67 seasons. The sample number and reason for omission are given in each case. No stomachs were taken from animals in parklike jackpine. The legend is given in Figure 29.



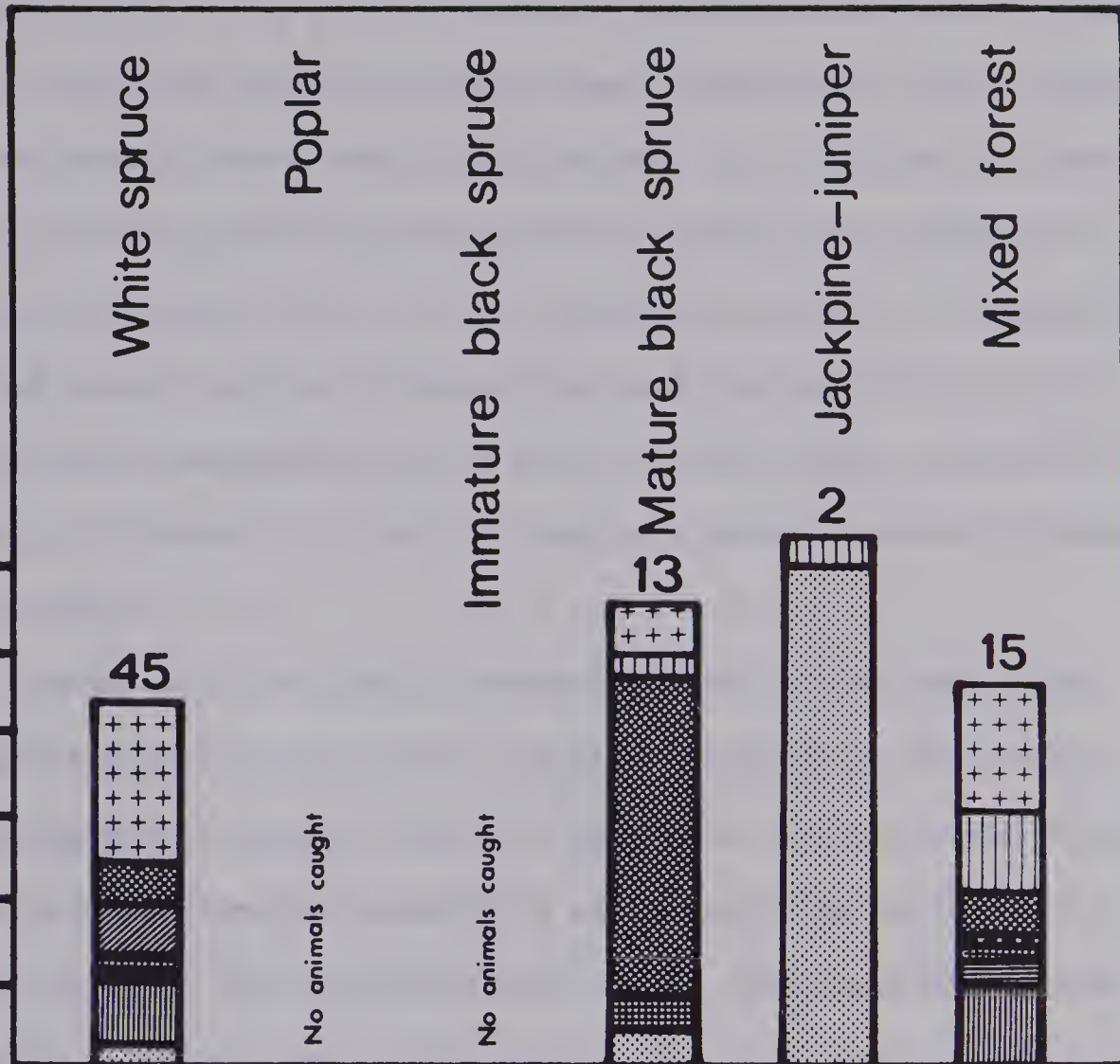
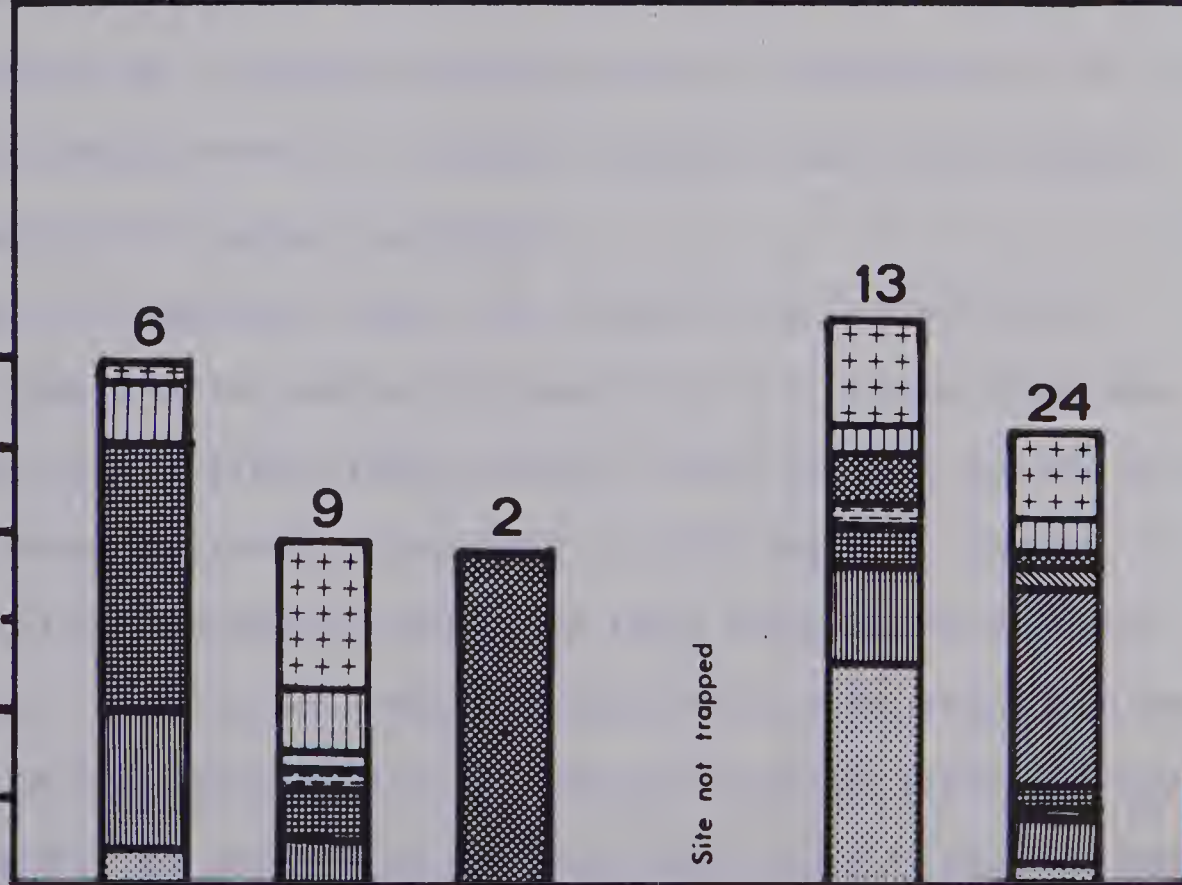
Volume (ml.)

C. gapperi

C. rutilus

1.2  
1.0  
.8  
.6  
.4  
.2

1.2  
1.0  
8  
6  
4  
2





"Mixed forest" is the group into which donated stomachs were placed (although a few fitted into the regular plant communities), and consisted mainly of mixtures of white spruce and jackpine in *C. gapperi* territory with some pure white spruce faciations of an island in the Mackenzie River off Fort Providence (Fig. 2) in *C. rutilus* territory. Because of the mixed and general nature of these sites and the similarity of the subsequent dietary composition to the basic regimens (Figs. 29 and 31) this category in Figures 33-35 may be used as a rough standard of comparison for the others.

For *P. maniculatus* the largest stomach volumes by far were taken from the jackpine-juniper stand of *C. gapperi* territory in the spring period, and represents food of animals trapped too near the field station. It is suspected that the high quantities of unidentified material in these stomachs is lab chow, including sunflower seeds. This species consumed insects mostly in white spruce of *C. rutilus* territory and in poplar and jackpine-juniper of *C. gapperi* territory; and ate mushrooms only in the mature black spruce stand of *C. rutilus* territory and in the jackpine-juniper forest of *C. gapperi* territory.

Mice ate low preference (Figs. 24, 25 and 27) *R. woodsii* and *S. canadensis* fruits in the various biotopes (Fig. 33) in quantities less than biotopic availability (Tables 6 and 7) would suggest; and ate relatively preferred fruits of *A. uva-ursi*, *V. vitis-idaea*, *G. lividum*, *R. strigosus* and *F. virginiana* in what were large quantities considering availability. These latter foods were found in stomachs roughly in proportion to biotopic availability, but often in stomachs taken from biotopes where the fruits did not grow at all (Fig. 33). Thus, *A. uva-ursi* fruits were eaten by animals taken from the mature black spruce stand; *V. vitis-*





*idaea* fruits by those from the poplar, jackpine-juniper and parklike jackpine forests of *C. gapperi* territory; and *G. lividum* fruits by those from parklike jackpine of *C. rutilus* territory and biotopes of *C. gapperi* territory. *F. virginiana* fruits were found in low numbers inside the forests (Tables 6 and 7), but were found in especially large amounts in stomachs of animals taken in both sets of white spruce and poplar plots and jackpine-juniper of *C. rutilus* territory where the verges held an abundance of these fruits. *R. strigosus* fruits, which only grow in clearings and not in any of the biotopes, were found in large numbers in most *P. maniculatus* stomachs. Records of the nearest locations of extra-biotopic fruits indicate that movements of 30-120 m were necessary for their ingestion.

*Clethrionomys* spp. ate mushrooms in all but the immature black spruce stands and the white spruce stand of *C. gapperi* territory where they were scarce. Insects were found in stomachs of animals only from the white spruce site of *C. rutilus* territory.

The little preferred (Figs. 24, 25 and 27) fruits of *R. woodsii* and *S. canadensis* occurred in lower proportions in stomachs of *Clethrionomys* spp. than in the habitats (compare Fig. 34 with Tables 6 and 7). *A. uva-ursi* fruits were found in none of the *C. rutilus* stomachs and only in those of *C. gapperi* from jackpine-juniper. For the highly preferred fruits of *G. lividum* and *R. strigosus*, consumption conformed to biotopic availability. In spite of higher preferences for *F. virginiana* fruits in *Clethrionomys* spp. than in *P. maniculatus*, these occurred in small amounts in *Clethrionomys* stomachs and only in biotopes where they were abundant and in the white spruce stand of *C. rutilus* territory which had a productive verge.





*Clethrionomys* spp. also ate the highly preferred (Figs. 24, 25 and 27) *V. vitis-idaea* fruits, which are especially important in the spring diet, in proportion to availability (compare Figs. 34 and Tables 6 and 7). In biotopes where these fruits were unavailable (e.g. white spruce, poplar, mixed) the voles resorted to consumption of greater volumes of low preference foods such as insects, arboreal lichens, leaves and *R. woodsii* fruits. Voles also yielded stomachs with greater "unidentified" portions in sites devoid of *V. vitis-idaea* fruits.

Locally obtainable species of leaves were represented in *Clethrionomys* stomachs. *R. chamaemorus* fruits made up a good portion of the "unidentified and others" category in the immature black spruce stands, the only sites where they occurred.

In general, *P. maniculatus* showed low consumption:availability ratios in the various biotopes for low preference fruits and a high ratio and high foraging activity for those of high preference. Stomach contents of *Clethrionomys* spp. reflected availability more.

For the winters of 1965-66 and 1966-67 (Fig. 35) the biotopic breakdown of the average stomach volumes of *Clethrionomys* indicates that *V. vitis-idaea* berries were eaten, for the most part, in the habitats where they were available (Tables 6 and 7), especially in the black spruce associations. But the fruits were even eaten to some degree by animals in habitats devoid of them (white spruce and *C. gapperi* jackpine-juniper). These fruits were not eaten as much as was expected in the jackpine-juniper stand of *C. rutilus* territory (Table 6) where mushrooms were plentiful (p. 66 and Fig. 34). In the biotopes lacking *V. vitis-idaea* fruits (Tables 6 and 7) and in areas where few mushrooms were consumed, there was a tendency for arboreal lichens, fruits of *R. woodsii* and unidentified



materials to be eaten in greater quantities (Fig. 35).

The only obvious difference between *C. rutilus* and *C. gapperi* consumption as a whole was the higher ingestion of *V. vitis-idaea* fruits, especially in winter (Fig. 35) and spring (Fig. 34) by *C. rutilus*, and the consequent substitution of less preferred fruits in *C. gapperi* (see also Fig. 29). However, when the mixed forests, which are assumed to be averages, are compared, it is seen that this difference is probably due to the choice of biotopes (see availability values in Tables 6 and 7) and especially to the inclusion of mature black spruce in *C. rutilus* territory only. There were no general dietary differences between *P. maniculatus* from the two territories.

The biotopic consumption data expressed as percentage frequency (Appendix IX) is remarkable only in the generally high consumption rates of insects, arboreal lichens, leaves, feather mosses and *R. woodsii* fruits in *C. rutilus* stomachs from habitats where *V. vitis-idaea* fruits were scarce and relatively low rates in the mature black spruce stand where they were most plentiful. In winter stomachs of *Clethrionomys* spp. greater frequencies of arboreal lichens, *R. woodsii* fruits and unidentified materials are seen for sites lacking *V. vitis-idaea* (Appendix IX).

An inexplicable feature of *P. maniculatus* consumption in jackpine-juniper (*C. gapperi*) is the high frequency of occurrence (significant in all cases) of many little-preferred (Figs. 24, 25 and 27) foods such as mushrooms, *Parmelia* spp., feather mosses, leaves, and the fruits of *R. woodsii* and *V. vitis-idaea*.

The trophic relationships of the animals to the various biotopes may now be summarized:





Biologically, opportunism was reflected more in vole food habits, notably in their tendency to substitute less preferred "rougher" foods for the much preferred overwintered fruits of *V. vitis-idaea*: more extensive foraging excursions seem to characterize mouse food habits (see also Fuller, 1969b). These differences were also evident from the biotopic heterogeneity in the diet of the former as opposed to the relative uniformity of the latter (compare Fig. 34 with Fig. 33). The ability of *Clethrionomys* spp. to shift its diet annually was also demonstrated above.

### Density Variations

In this section changes in rodent numbers are presented in turn from seasonal, annual and biotopic aspects.

Seasonal variation. The structure of the fauna in the several habitats changed throughout the summer months (Fig. 36). Numbers in immature black spruce and parklike jackpine forests of *C. gapperi* territory were seasonally constant and very low. For this reason, and because these areas contained only one species each, they are not represented in the figure. The expansive white spruce forest in *C. rutilus* territory was intensively trapped in 1965 and 1966, and these results represent this site exclusively in the figure. Values from 1965 are represented only for mature black spruce (*C. rutilus*) and jackpine-juniper (*C. gapperi*). Otherwise, the values are averages of 1966, 1967 and 1968 values. Since, in May, only a few trapping rotas were performed in the last half of the month, these results were incorporated into the June indices.

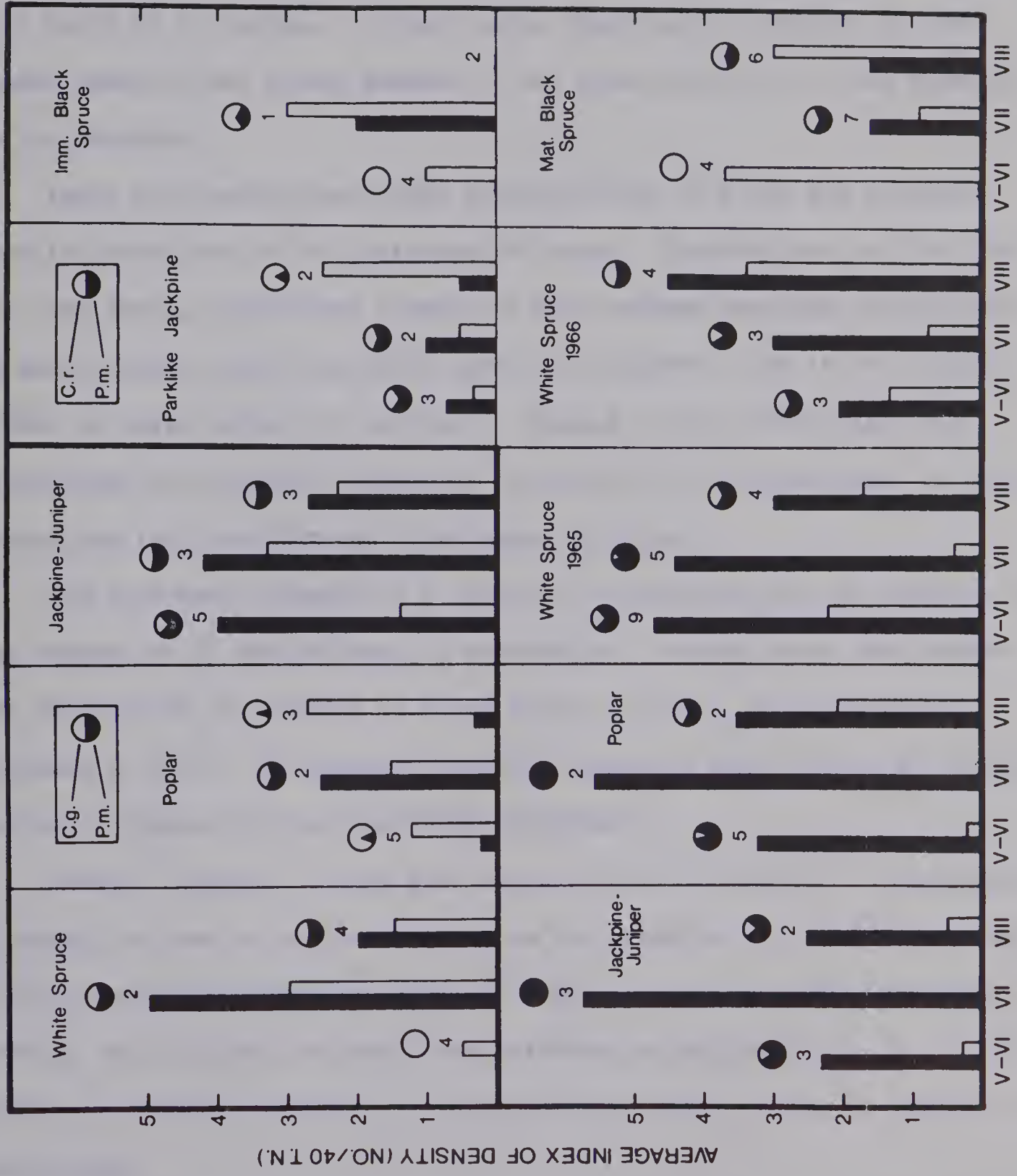
Peak numbers of *P. maniculatus* in July were only significantly greater ( $p < 0.05$  between June and July;  $p < 0.025$  between July and August) in







Figure 36. Seasonal variation in the absolute (vertical bars) and relative (pie diagrams) faunal compositions of nine plant communities. *C. gapperi* territory, minus two omitted communities, is set off by dark lines at upper left. Black=*Peromyscus*; white=*Clethrionomys*. The numbers shown above the bars represent the number of times the area was sampled. May and June values are combined.





*C. gapperi* territory as a whole. Collectively, July maxima were generally significant ( $p < 0.05$ ) in *C. gapperi*, whereas July minima were significant ( $p < 0.01$ ) in *C. rutilus*. In most cases there was an increase in late summer numbers over spring numbers in the voles, but this is not apparent in the deermice.

There are insufficient index determinations to bring out seasonal density variations in the individual biotopes. Nevertheless, at the five per cent level, significant changes in vole numbers occurred in June-July in mature black spruce and white spruce (*C. gapperi*), and in July-August (1966) in white spruce (*C. rutilus*). Changes in mouse densities were significant in *C. gapperi* territory for June-July and June-August in white spruce and for June-July and July-August in poplar.

The midsummer decrease of *C. rutilus*, concomitant with an increase in the numbers of *P. maniculatus*, is remarkable. In most cases this change was followed by an increase of voles again in August and a concurrent decrease in mice. The sparsely-populated immature black spruce and parklike jackpine biotopes did not show this phenomenon.

Among *C. gapperi*, a July peak was realized with that of *P. maniculatus*. Although this was in direct contrast to the dynamics of *C. rutilus*, examination of the pie diagrams in Figure 36 shows a decrease in the vole:mouse density ratio in July in every case, although significantly so ( $p < 0.05$ ) only in *C. rutilus* territory as a whole and in white spruce (*C. gapperi*) in particular.

Annual variation. Figure 37 shows annual density indices for the allopatric *Clethrionomys* spp. and for the *P. maniculatus* population associated with each species. To account for unequal sampling frequency, the means were determined from sub-averages and, thus, are equally weighted for

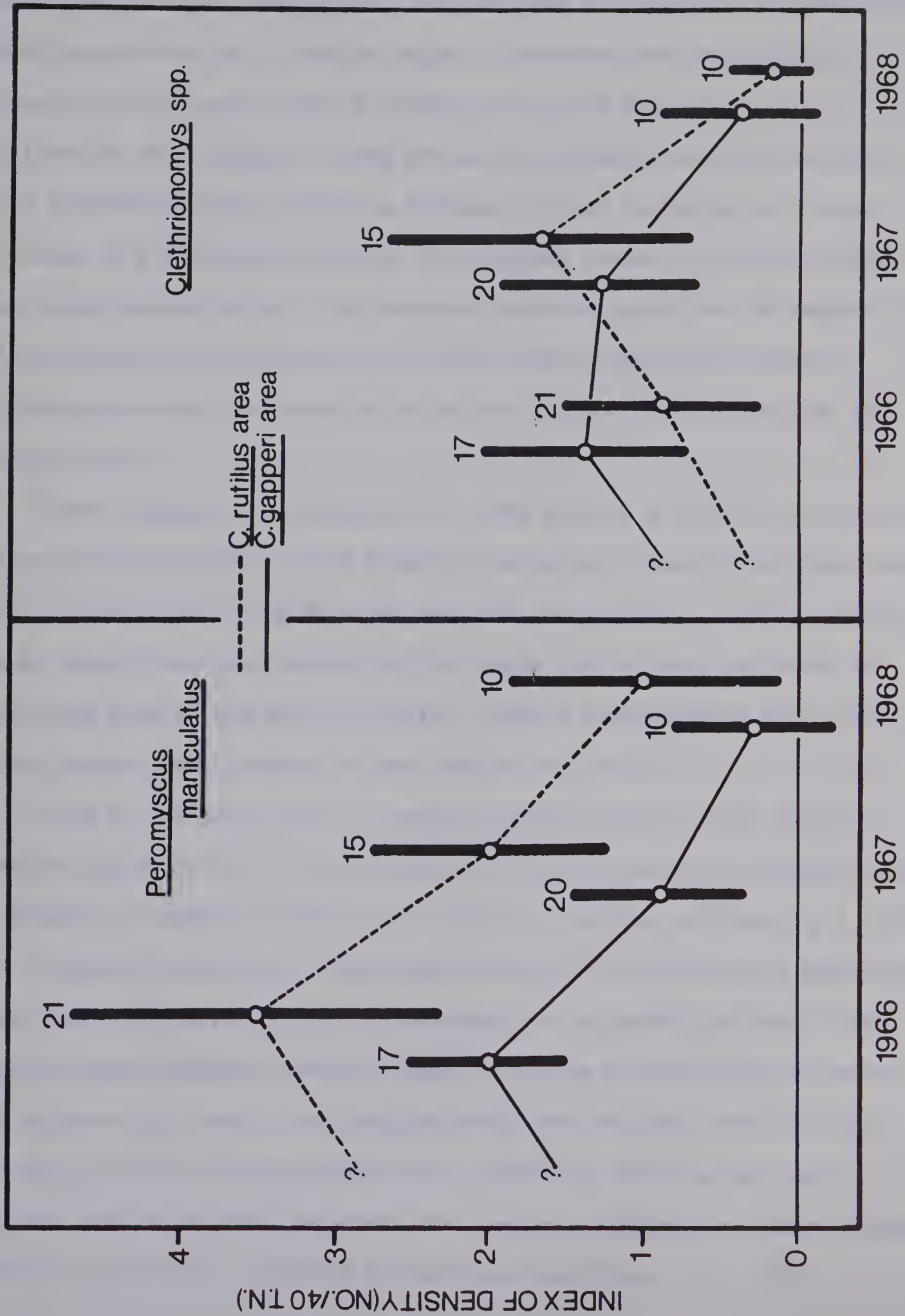






Figure 37. Annual variations in density of the three cricetids.

The means are averages of values equally weighted for season and biotope. The 95 per cent confidence interval was determined from *within-biotope* variation only. The number of censuses is indicated for each year. Dashed lines indicate *C. rutilus* territory and solid lines *C. gapperi* territory.





season and biotope in each year. For the same reason, mature black spruce, which occurs only in *C. rutilus* range, is omitted from this synopsis. Because of the great extent of biotopic variation the range is not included in the graph and the 95 per cent confidence intervals are based only on *within-biotope* variation (*between-biotope* variation was removed by means of a one-factor analysis of variance) caused by seasonal change and "experimental error." The seasonal variation could not be removed without drastically reducing the *within-biotope* degrees of freedom. Significance tests are based on the *within-biotope* variance and the full sample number.

Since trapping was carried out in 1965 only in a few of the regular sites, and otherwise in mixed forests, the index of density for that year is not commensurate with those of the next three years. There is little doubt though that fewer animals of all three species were available in that year than in the next, and Fuller (1969a) substantiates this. Even lower numbers were present in 1964 (Fuller, *op. cit.*).

Both *P. maniculatus* and *C. gapperi* reached peaks in 1966 while *C. rutilus* peaked in 1967. *P. maniculatus* in both territories decreased significantly in numbers in 1967 ( $p < 0.02$  in *C. rutilus* territory;  $p < 0.005$  in *C. gapperi* territory). The further decrease in 1968 was not significant, but since it occurred in both territories, it is probably a fact. The *C. gapperi* index does not show the dramatic decline in 1967 that was sensed by Fuller's (*op. cit.*) live-trapping study, but the 1968 drop was significant ( $p < 0.05$ ). The increase of *C. rutilus* in 1967 was not quite significant at the five per cent level, but was confirmed by other evidence (Fuller, *op. cit.*). The 1968 decrease was significant ( $p < 0.02$ ).





For any given year there were no significant differences between the numbers of the two voles. Fuller (*op. cit.*) estimated similar densities for *C. rutilus* and *C. gapperi* at the end of the 1966 season, but he found differences in 1967 when *C. gapperi* numbers declined while those of *C. rutilus* increased by about 50 per cent.

Of the two populations of *P. maniculatus*, the one in *C. rutilus* territory was significantly denser in 1966 ( $p < 0.005$ ) and 1967 ( $p < 0.02$ ), and probably in 1968. Fuller (*op. cit.*) found much higher *absolute* densities in *P. maniculatus* sympatric with *C. rutilus* but ascribed this phenomenon to the unsuitability of two of his plots. This explanation will be investigated for the present study also.

Biotopic variation. The cricetid composition of the habitats was determined from trapping in the summers of 1966 and 1967. Only two communities were trapped in 1965 and in 1968 hardly any animals were caught. Mean indices were determined from sub-averages (May-June and July-August for the two years) to eliminate the biases of heavy or light censusing frequencies. However, these corrected means never differed more than 0.8 per 40 trap-nights from the "straight" means, seldom more than 25%, and often did not differ at all.

The biotopic densities are represented in Figure 38 in an idealized sequence of seral stages as a reminder of the long-term density fluctuations and changes in faunal structure which community succession may effect. White spruce, the potential climax forest of the taiga, is shown on the corner with the jackpine-poplar sere on the left and the black spruce sere on the right. It should be emphasized that neither cricetid composition nor any of the other attributes of these communities are considered typical of the sere at that particular stage of succession.

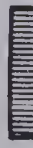



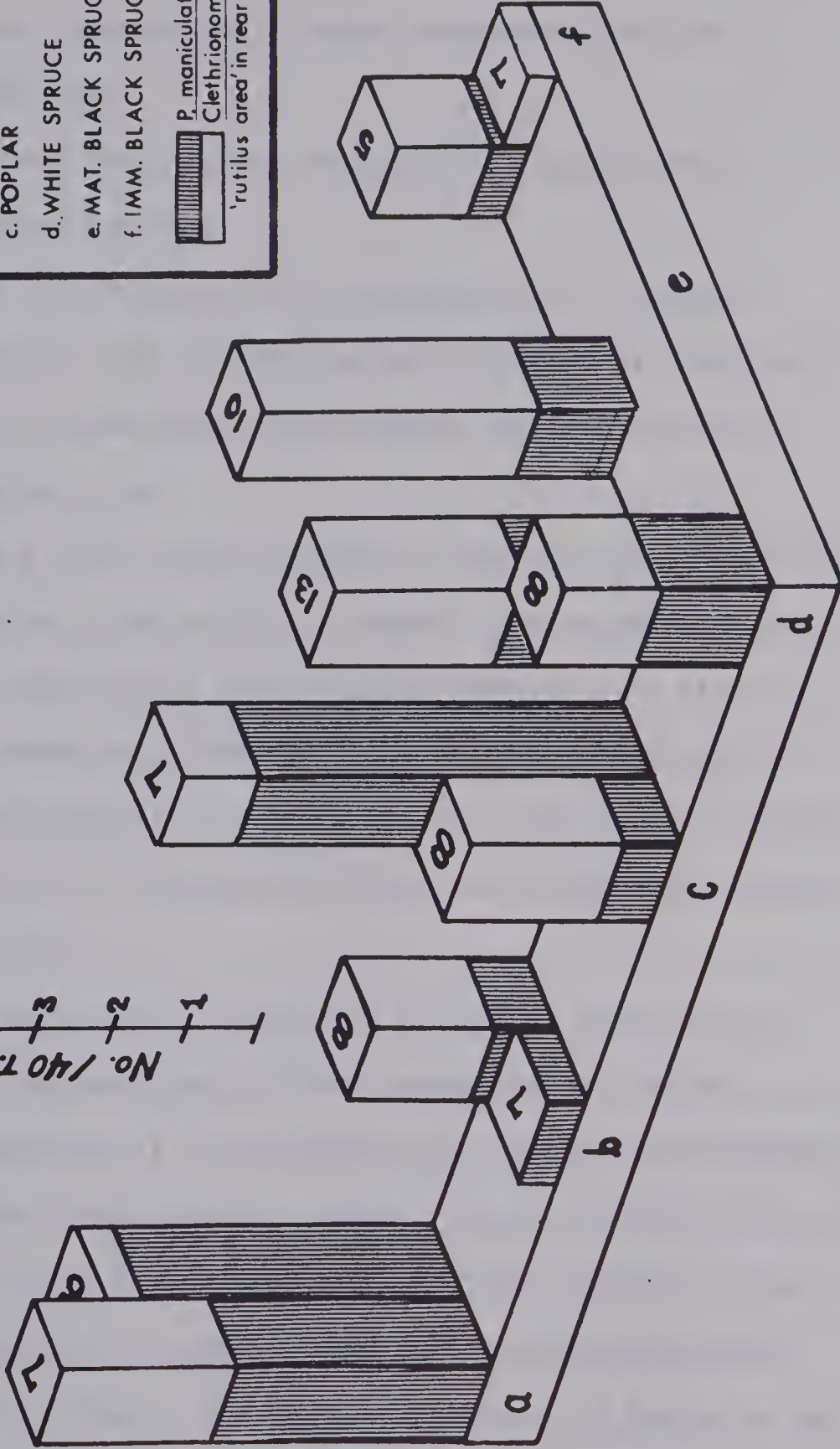


Figure 38. Faunal compositions of the plant communities. Means are averages of values equally weighted for season and year. Numbers on the tops of the columns represent the number of censuses on which means are based.

No. / 40 T.N.  
1  
2  
3  
4

- a. JACKPINE - JUNIPER
- b. PARKLIKE JACKPINE
- c. POPLAR
- d. WHITE SPRUCE
- e. MAT. BLACK SPRUCE
- f. IMM. BLACK SPRUCE

 *P. maniculatus*  
 *Clethrionomys*  
 'rutilus area' in rear







Examination of the pattern of spatial densities suggests the following:

- 1) There is variation in faunal structure among the communities.
- 2) Immature black spruce and parklike jackpine were marginal habitats.
- 3) With the exception of the marginals of *C. gapperi* territory both subfamilies were found in all habitats. This included mixed forest whose densities are not examined here.
- 4) In all cases there were more *P. maniculatus* in *C. rutilus* territory than in the *C. gapperi* counterparts, whereas the overall vole densities were similar (see also Fig. 7).
- 5) The three basic vegetation types (p. 57) had three characteristic faunal structures; black spruce associated with voles, jackpine with mice, and white spruce-poplar with both.
- 6) The poplar stand within the *C. rutilus* range and the two jackpine-juniper stands supported the largest populations of *P. maniculatus* (no significant difference between these latter). These, along with the white spruce and mature black spruce of *C. rutilus* territory, also supported the highest total numbers (no significance between them). The habitat preference of the voles was greatest for mature black spruce.
- 7) Jackpine-juniper stands had higher numbers of mice than voles ( $p < 0.05$  for *C. rutilus*). The white spruce stands showed similarity in that they supported equal numbers of



mice and voles, but each of the genera of the *C. rutilus* territory was twice as dense as in the counterpart stand in *C. gapperi* territory. The poplar stands had opposite faunal structures, mice being much more plentiful than voles ( $p < 0.001$ ) in *C. rutilus* territory and voles less plentiful (not quite significant) in the other. In mature black spruce voles represented a significantly greater proportion ( $p < 0.05$ ) of the fauna than did mice. Within the *C. gapperi* area only a few mice were found in parklike jackpine and a few voles in immature black spruce (no significant difference). Their complements in *C. rutilus* territory, however, had a significantly greater ( $p < 0.05$ ) total population composed in each case of one-third mice and two-thirds voles. Only in parklike jackpine were voles significantly more plentiful ( $p < 0.05$ ) than mice.

To bring out biotopic variations in population characteristics other than density requires greater numbers than were available for this study, preferably collected concurrently. From the data on hand, however, there do not appear to be any differences between the sites in the weights of animals. That the animals of the marginal habitats seem to have similar body weights to the rest of the study area in spite of their smaller stomach volumes (Figs. 33-35) indicates that the ones caught there may not have been residents. To further support this speculation sex ratios, which were generally only slighter in favor of males in all three species (Fuller, 1969a), were very strongly so in some of the marginals. Thus, in *C. rutilus* territory 91 per cent male mice and 50 per cent male voles were



found in parklike jackpine, and in immature black spruce 100 per cent male voles and 50 per cent male mice were caught. In *C. gapperi* territory, 75 per cent male mice and no voles were taken in parklike jackpine, and 67 per cent male voles and no mice were taken in immature black spruce. If males show wider movements than females, these high male ratios may indicate that the sites yielded many transients.

In order to quantitatively test the importance of food it was necessary that each habitat be given two numerical assessments, one for each genus (since preference values of the two species of *Clethrionomys* are similar). These values were obtained by weighting food availability with the appropriate preference index, thus:

$$\begin{aligned} & (\text{availability of food A} \times \text{preference index of A}) + \\ & (\text{availability of food B} \times \text{preference index of B}) + \dots \\ & + (\text{availability of food n} \times \text{preference index of n}) \\ & = \text{trophic habitat value.} \end{aligned}$$

Because of the ubiquity, abundance and low preference of vegetative foods, they are not considered of importance in quantifying forest habitats (at least in the summer season). The highly preferred leaves of sapling *P. tremuloides* were absent in the forests and, thus, cannot be considered.

Since mushrooms are fairly cosmopolitan when present, only production of fruits is weighted with their preference values to analyze biotopic numbers. It has been shown (Figs. 29-35; Table 16 and Appendices VII, VIII and IX) that fruits make up the major part of the diet in the period presently under concern. The "weight" index is used because it is assumed to be commensurate within the fruit category of foods.

When densities were plotted against these assessments the simple correlation coefficients were found to be  $r=+0.17$  and  $r=+0.13$  for *P. maniculatus*







and *Clethrionomys* spp. respectively (Table 17).

Besides food, Table 17 shows simple correlation coefficients for the aspects of cover (Table 9) and for the sympatric rodent. The coefficients for the cover parameters are high, and indicate that the numbers of *P. maniculatus* are associated with frequency of fallen trees while *Clethrionomys* are found in habitats with highest foliage cover. These relationships which *a priori* were considered linear by nature, are given in Figure 39. The dissociated points in this figure indicated by the arrows are those of the jackpine-juniper site which are omitted from computations because "artificial" foods were found in the diet of *P. maniculatus* in that area. That these points are unusually high on the y-axes is in itself indicative of some food influence on density, albeit artificial.

Also in Table 17, within the aspects of cover, which parameters appear to be the most important, some statistical control is exerted through partial correlation. This process, which involves holding other independent variables constant, emphasizes the superiority of the "fallen trees" variable for mice and "foliage cover" for voles. The multiple correlation values of Table 17 take all three cover correlates into account.

Biotopic densities and cricetid make-up showed peculiarities with annual changes in numbers (Fig. 40). The *P. maniculatus* peak in 1966 was associated with decreased *C. rutilus* numbers in jackpine-juniper, poplar and white spruce in decreasing magnitude. The *C. rutilus* peak of the following year (1967) allowed these animals to increase their numbers in these biotopes in increasing magnitude. Also in 1966 *C. rutilus* increased dramatically ( $p < 0.001$ ) in the mature black spruce stand. Marginals appeared to be used most in high years.

These dynamics were not as obvious in *C. gapperi* territory.



Table 17. Simple correlation coefficients of biotopic densities with several environmental components and the second order partial, and multiple, correlation coefficients for the three cover parameters. The jackpine-juniper stand of *C. gapperi* territory is eliminated for reasons given in the text.

Density (1)	Food (2)	Fallen Trees (3)	Litter (4)	Foliage Cover (5)	The Other Animal (6)	Multiple Correlation
<u>Mice</u>						
Simple	$r_{12} = 0.17$	$r_{13} = 0.88$	$r_{14} = 0.77$	$r_{15} = 0.13$	$r_{16} = -0.04$	
Partial and Multiple		$r_{13.45} = 0.71$	$r_{14.35} = 0.33$	$r_{15.34} = -0.02$		$R_{1.345} = 0.90$
<u>Voles</u>						
Simple	$r_{12} = 0.13$	$r_{13} = 0.19$	$r_{14} = 0.20$	$r_{15} = 0.70$	$r_{16} = -0.04$	
Partial and Multiple		$r_{13.45} = 0.01$	$r_{14.35} = 0.00$	$r_{15.34} = 0.75$		$R_{1.345} = 0.84$





Figure 39. Density indices plotted against fallen tree frequency for *P. maniculatus* and against amount of foliage cover for *Clethrionomys* spp. The points indicated by the arrows are omitted from the regression calculations for reasons given in the text.



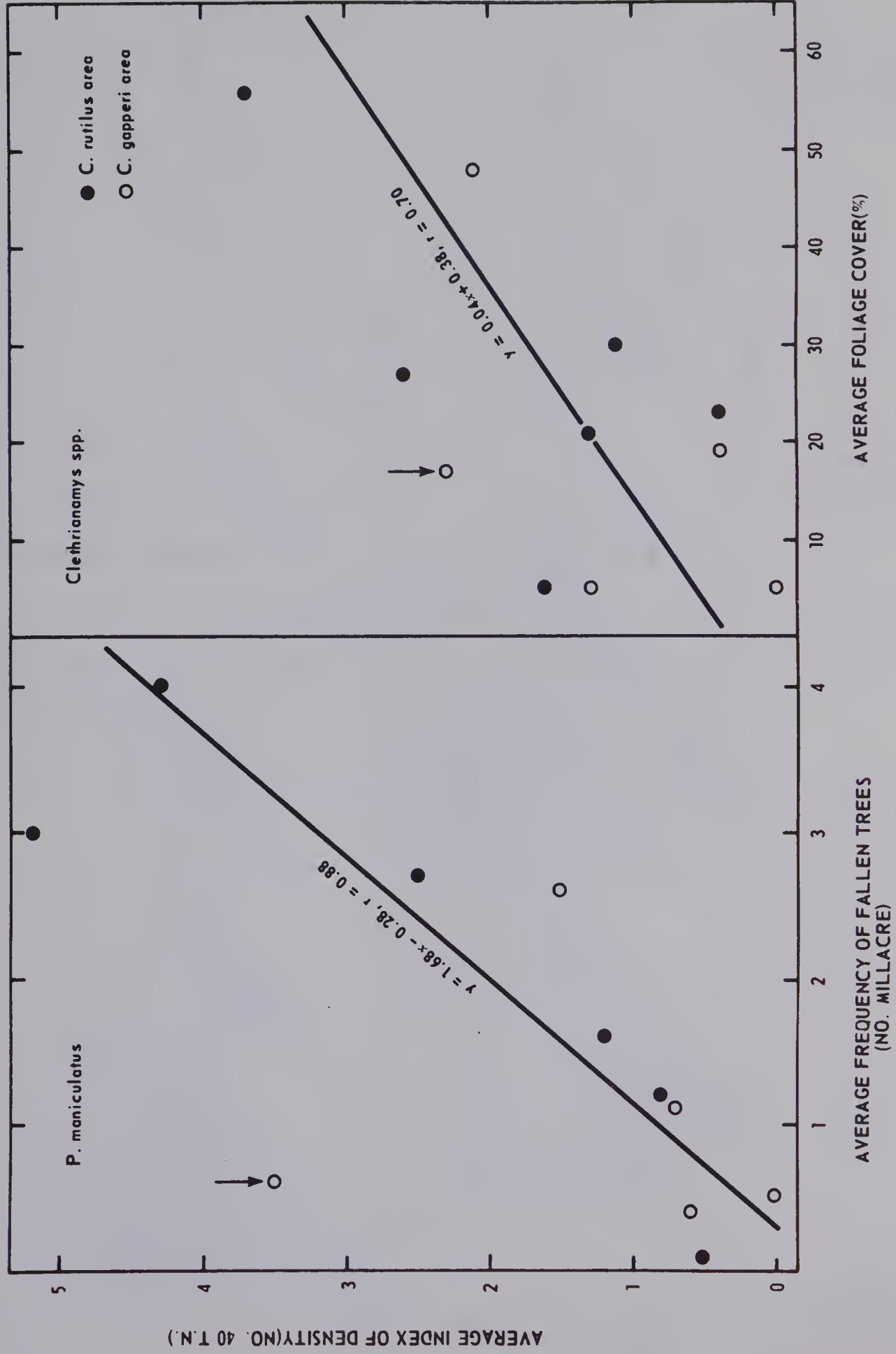



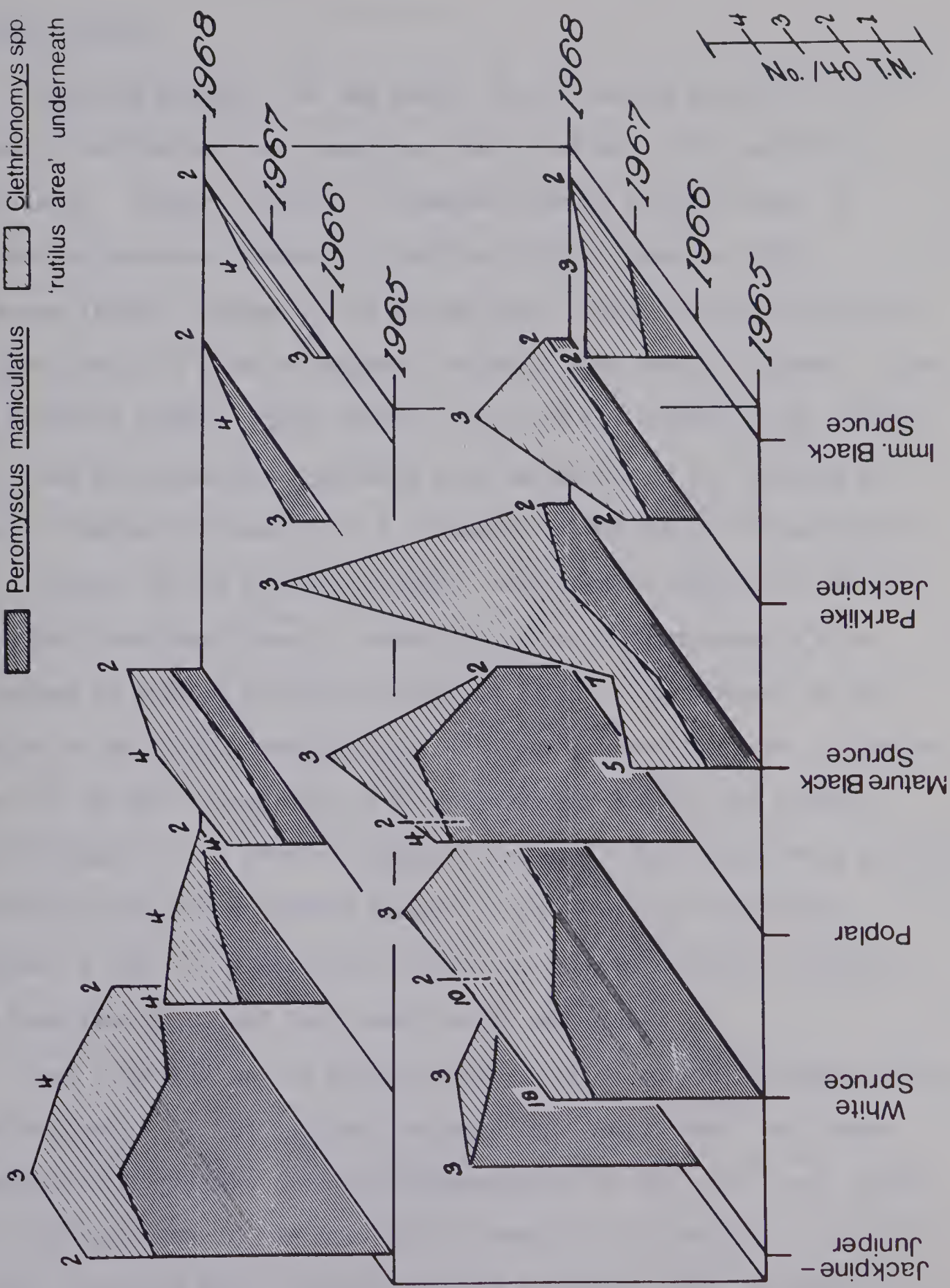






Figure 40. Faunal compositions of the plant communities showing annual variations in mouse and vole densities. Means are averages equally weighted for seasons. The x-axis represents biotopes; the y-axis, density; the z-axis, the year. The number of censuses on which the averages are based is given for each year and biotope.

 Peromyscus maniculatus  
 Clethrionomys spp.  
 'rutilus area' underneath



N. 1. 04  
 No. 140 T.N.





## DISCUSSION

### Trophic Niches

The study animals. On the whole, the literature provided little specific information concerning food habits of any of the animals of this study. Stomach contents of temperate North American races of *P. maniculatus* were examined by Hamilton (1941), Jameson (1952), Williams (1959), Johnson (1961) and Whitaker (1966) and investigations on food habits of captive temperate deermice were made by Cogshall (1928) and Menhusen (1963). These studies disclosed the animals to be omnivorous, with the proportions of major food categories (i.e., insects and fruits) similar to those of *P. m. borealis* of the present investigation; but, contrary to the present findings, seed kernels appeared to be more important than fruit flesh. Insect predation by *Peromyscus* is also described by Holling (1959) and Kendeigh (1961). In contrast to the results of my study, Kendeigh (*op. cit.*) and Johnson (*op. cit.*) reported grass to be part of the diet of *P. maniculatus*; and all the studies reported above, save that of Hamilton (*op. cit.*) found vegetative material, including roots and succulent leaves, to be of dietary importance. Cogshall's (*op. cit.*) mice were similar to mine in that they ate buds and bark from stems and left woody tissue untouched.

Even less work on the dietary patterns of *C. gapperi* in North America has been done. In New England, Hamilton (*op. cit.*) found that summer stomachs of *C. gapperi* contained approximately 75 per cent green vegetation and more than 10 per cent insect remains. The remainder consisted of nuts, seeds of *Rubus*, *Amelanchier* and *Vaccinium*, and some fungi. In earlier studies in the New England area, Merriam (1884) and Rhoads (1903)



did not find insects in vole stomach contents, but greater quantities of seeds and berries than did Hamilton (1941). Rhoads (1903) also determined that his animals were fond of certain shelled snails (*Omphalina* and *Polygyra*). In winter stomachs, Merriam (1884) found bark while Rhoads (*op. cit.*) found strawberry leaves to the exclusion of other foods. Sharp (1965) found root material and fungal spores in *C. gapperi* stomachs of southern Alberta. In contrast to the results of the literature, the Mackenzie population of *C. g. athabasca* appears to be unique in its ingestion of great quantities of arboreal lichens, mushrooms and berry flesh, as well as in the essential absence of insect material in the diet.

The above review reveals that no literature concerning the food habits of northern new world races of the study animals is available. Therefore it is necessary to compare the results of this study concerning the diet of *C. rutilus* (which species does not occur elsewhere in North America) with those of old world investigations.

In northern Russia *C. rutilus* was found to consume lichens (mainly *Bryopogon*) and small amounts of greenery in spring with those foods declining in importance in August as berry consumption increased (Koshkina, 1957). Insectivory was common and mushrooms were eaten in large quantities where present. For the same species, Vorontzov (1961) and Shtil'mark (1965) observed very similar consumption patterns except that, instead of the large vernal consumption of highly preferred lichens which Koshkina (*op. cit.*) reported, their animals consumed more achlorophyllous and chlorophyllous material. Feather moss, which Koshkina (*op. cit.*) considered a "constant and unlimited source of food," was eaten infrequently and in trace amounts by her animals, whereas Shtil'mark (*op. cit.*) considered it an important nutritional base, especially in autumn, winter and early



spring. *C. rutilus* of the present study ate feather mosses and arboreal lichens in quantities and frequencies much as described by Koshkina (1957) and differed from all the animals described above in not being insectivorous and eating overwintered fruits in spring.

Nematodes, because they occurred whole in the vole stomachs, and only in adults, are probably parasites and not food items.

Old World equivalents. Rausch and Tiner (1949) considered the European murid, *Apodemus*, to be in some ways comparable to the North American *Peromyscus*. Walker *et. al.* (1964) refer to this similarity as a "striking convergence . . . in shape, appearance and habits." Elton (1942) called *A. sylvaticus* "a form not unlike the American deermice (*Peromyscus*) in its general appearance and habits." Similarly, the European and American species of *Clethrionomys* may be shown to be ecological equivalents in that the relations of mice to voles on each continent are similar as far as home range (compare Bergstedt, 1966 to Burt and Grosenheider, 1954 and Beer, 1961), activity (compare Buchalczyk, 1964 to Stebbins, 1968), gastrointestinal apparatus (compare Gorécki and Gebczyńska, 1962 with Fig. 1) and, perhaps, dominance (Andrzejewski and Olszewski, 1963 to the circumstantial evidence of the present study discussed below) are concerned. An assumption of ecological equivalence will prove useful throughout the following discussion.

As was found in the current study, Drożdż (1967) found no difference between voles (*C. glareolus*) and mice (*A. flavicollis*) in Poland in their preference for seeds and fruits, but his voles ate three times as much "herb layer" vegetation. However, *C. glareolus* in Russia studied by Vorontzov (1961) and in Czechoslovakia by Holišová (1966) ate much more greenery (including moss) with much less mushroom and lichen than the







voles of the present study. The data of Miller (1954) from Britain suggest that, except for *C. glareolus* eating animal matter in substantial quantities and little mushroom as compared to *C. gapperi*, *A. sylvaticus* and *C. glareolus* are trophically related in the same manner as *P. maniculatus* and *Clethrionomys* spp. Insectivory in *C. glareolus* was also witnessed by Holířová (1966) in the Czechoslovakian lowland forests and by Droždž (1967) in Poland, but not in northern Russia by Koshkina (1957) and Vorontzov (1961).

In Russia, Koshkina (*op. cit.*) found that *C. glareolus* eats lichens (predominantly *Bryopogon*, but not *Parmelia*) in the winter, spring and first half of the summer and a few mushrooms in late summer. Vorontzov's (*op. cit.*) studies, however, revealed less lichen material in the diet and more mushroom. Both workers found berries to be important in late summer at which time the normally slight amounts of greenery disappeared from the diet altogether.

Koshkina (*op. cit.*) and Kalela (1957) both studied the food habits of *C. rufocanus*, in Russia and Finland respectively. For the spring diet of the animals, Koshkina (*op. cit.*) reported a high level of lichen consumption whereas Kalela (*op. cit.*) did not. The spring and summer diet of Koshkina's and Kalela's animals consisted of quantities of a great variety of leaves and stems, and the fall diet of berries. Mushrooms were eaten by Kalela's animals in the rainy seasons, but not by Koshkina's. Because *C. rufocanus* consumes a highly diversified diet of chlorophyllous parts and can actually subsist wholly on greenery (Koshkina, *op. cit.*), this species does not resemble *Clethrionomys gapperi* and *rutilus* closely in diet.

It appears that, with a few variations, *Apodemus* and *C. glareolus*



are equivalent in diet as well as in other attributes to *P. maniculatus* and *Clethrionomys* spp. of the present study. The consumption of both bulky and concentrated foods by voles and mainly concentrated foods by mice (Drożdż, 1966) sums up the trophic essentials of these sympatric pairs.

Reliability of indirect investigations. Comparisons of actual diets with the introductory speculations (see THE ANIMALS) may now be made. Dental characteristics did not indicate the equal degree of frugivory discovered for the three species, nor anything of mushroom consumption. Although the consumption of vegetative foods by *Clethrionomys* was correctly predicted from morphological and behavioral criteria, the proportions and patterns of such consumption were not indicated. Similarly, "remains" or "leavings" around nests and burrows (Hamilton, 1941, Kalela, 1957; Blus, 1966) are not necessarily foods and should not be strictly interpreted as such. Therefore, I feel that indirect evidence should not be substituted for direct evidence when determining food habits and seeking to describe ecosystems.

Activity and food habits. Outside of the reproductive season at least, a large part of rodent activity is probably connected with feeding, which is why Naumov (1948) could associate three daily activity patterns with food habits of voles and mice. Thus, (1) granivorous mice (*Apodemus flavicollis*, *A. sylvaticus* and *Mus musculus*) are strictly nocturnal and are active for periods of three to five hours during the summer night and up to two hours during the winter night; (2) herbivorous voles (*Microtus arvalis*, *M. agrestis*, *M. oeconomus* and *Phenacomys subterraneus*) are active both day and night for periods of up to five or seven hours daily; and (3) polyphagous mice and voles (*C. glareolus*, *C. rufocanus*, *A. agrarius* and *M. minutus*), are predominantly nocturnal, and are active for up to



five hours in summer and two to four hours in winter. An ecological equivalent in the southern Mackenzie area, *P. maniculatus*, according to the food habit information gathered by myself and the natural activity patterns determined by Stebbins (1968), should fall into the first group, although Naumov (1948) makes no reference to insectivory in this category. *C. rutilus* and *C. gapperi*, on the other hand, lacked insectivory in the Mackenzie populations, but still fit best into the third group.

In terms of movement, *Apodemus* has a greater individual area than *C. glareolus* (Bergstedt, 1966). This may be so for their American counterparts (Beer, 1961), although movements of *C. gapperi* may have been underemphasized (Audrey Bodner, *pers. comm.*). The lack of biotopic studies in the old or new worlds makes it impossible to tell if the mouse is less opportunistic in food habits than the vole, as a larger home range would indicate. However, in England, Prof. K.R.Ashby (*pers. comm.*) believes food to be responsible for the long round trips made by *A. sylvestris*.

That wider-ranging less-opportunistic *P. maniculatus* of the present study ate less both totally and per gram body weight than *Clethrionomys* spp. (determined for lab chow only) seems inconsistent unless they have a more efficient alimentary system and metabolism. That they are capable of maintaining weight on foods eaten in small amounts (Fig. 28) also suggests this interpretation. In this regard, note that these mice are more hardy at withstanding lab conditions than voles (Dyke, 1970). *Clethrionomys* is expected *a priori* to eat more than *Peromyscus* in the light of its capacious digestive tract (Fig. 1) which in the natural environment is necessary for processing foods (such as those of Figure 29) of low usable energy ("roughages") in relatively enormous quantities to







obtain the energy and nutrients necessary for normal maintenance and production (Crampton and Lloyd, 1959). But Prof. K.R. Ashby (*pers. comm.*) found that *A. sylvaticus* requires less nutrient for maintenance than *C. glareolus*.

In Virginia *C. gapperi* consumes ten times as much water as *P. maniculatus* (Odum, 1944). Getz' (1968b) figures for *P. leucopus* versus *C. gapperi* in Connecticut are roughly similar to mine (Table 15). Urine of *P. leucopus* was 2.2 times as concentrated as that of *C. gapperi* (Getz, *op. cit.*) which is sufficient explanation for the generic difference in water turnover rate. These differences are expressed ecologically in the distribution of the animals, but their influence on overall activity is not understood.

No sexual comparisons could be obtained from the literature for *C. rutilus*, but it is agreed that *P. maniculatus* males have larger home ranges than do females (Storer, Evans and Palmer, 1944; Dice and Clarke, 1953; Fitch, 1958; and Stickel, 1968). Male *C. gapperi* also have larger home ranges than do females (Elliott, 1969). The present study indicates that adult non-reproductive males of all species eat, and probably drink, more than females in the laboratory (Tables 14 and 15). A comparison of surface to volume relationships suggests the opposite, but Prosser and Brown (1962) maintain that females have a greater proportion of tissues of low metabolic rate (such as fat) than do males of the same size. Reproductive females, however, were found in this study to have a higher natural spring consumption than males. Reproducing and lactating *P. m. bairdii* have been shown to require more water than males (Lindeborg, 1950). As for sexual differences in diet, Holířová (1966) reported that *C. glareolus* females ate large quantities of green material whereas in autumn



and winter males ate underground and surface parts (bark, etc.). In the same species Myrcha (1964) even found sexually-active females to have a larger alimentary tract. Sexual differences in preference were also discovered by Myers and Vaughan (1965) in gophers (*Thomomys talpoides*), and were attributed to "different metabolic and nutritional demands or different behaviour associated with the reproductive cycle." Similarly, female rats show a higher preference for sweetness (Baumgardt, 1969). Rand (1952) suggested that differences in food habits between males and females make it possible for the two sexes to live together more comfortably in a small area than if their requirements were absolutely identical. In the current study only quantitative sexual differences in food habits were found (Fig. 30), attributable to quantitatively different metabolic demands.

Finally, grooming activity may explain the presence of hair in the stomach contents of my animals. Johnson (1961) commonly found mammalian hair in the stomachs of *P. maniculatus* and assumed it came from the animal itself. Holíšová (1968) stated that balls of fur in the stomachs of dormice (*Glis glis*) were "obviously swallowed during grooming."

Torpor. Hamilton (1941) reported active storing of food by *P. maniculatus* and *C. gapperi* in the fall. For the present work, in the absence of evidence of food storage in nature, we must assume direct gleaning of foodstocks during winter when the energy budget demands extreme economy. Not only is food scarcest in this season but the need for it is critical because of low temperatures (Dice, 1922; Rowan, 1925; Howard, 1949 and 1951; Westerskov, 1964; Hafez and Dyer, 1969; Flatt and Moe, 1969) and less feeding time (Stebbins, 1968). The low winter stomach volumes (Fig. 30; also compare Figs. 34 and 35) of this study may represent reduced ingestion resulting from environmental lack, or from "Dehnel's phenomenon"—reduced



body size in winter presumably to conserve total energy requirements (Fuller, Stebbins and Dyke, 1969).

Torpor in *P. maniculatus* (Stebbins, 1968) is another energy-conserving mechanism. In comparing the winters of 1965-66 and 1966-67 Fuller, Stebbins and Dyke (1969) found that, contrary to the situation in *Clethrionomys* spp., *P. maniculatus* survived less well in the mild winter (1966-67). This was confirmed by Fuller (1969 ). These workers speculated that torpor as an adaptation to cold has its greatest survival value under extreme conditions because energy is not wastefully expended while torpor is induced. Thus, French, Bernardo and Aschwanden (1967) found a positive correlation between longevity of *Perognathus longimembris* and seasonal adversity.

The studies of Tucker (1962 and 1963) on *Perognathus californicus*, of Morhardt and Hudson (1966) on several species of *Peromyscus*, and of Davis (1967) on *Marmota monax* suggest that limited food supplies, not temperature, induce torpor which compensates for limited energy resources. Howard (1951) postulates that torpor in *P. m. bairdii* is an adaptation to reduce the amount of food required. Since the winter of 1965-66 was trophically inferior to that of 1966-67, the lower survival rate of 1966-67 may be as easily explained in terms of available overwintered fruits and insects in that winter (Fig. 31). High consumption may have inhibited torpor, increasing the probability of exposure, energy loss, and death. The ephemeral nature of the dietary components of *P. maniculatus* (fruits, insects) suggests that torpor is an adaptation to food lack. The more opportunistic *Clethrionomys* changes its diet to arboreal lichens and overwintered fruits.

Significance of sand ingestion. Horner, Taylor and Padykula (1964) speculated that sand in the stomach of the highly insectivorous grasshopper







mouse (*Onychomys torridus longicaudus*) is a "scouring device" activated by peristalsis to abrade soft tissue adhering to chitin fragments and render them available as useful particulate food. If that hypothesis is true, the insectivorous *P. maniculatus* would be expected to have sand in its stomach. If sand ingestion is an inherited trait, the evolutionary advantage of purposive sand-swallowing should be such that the entomophagous *P. maniculatus* would eat sand more often than the non-entomophagous *Clethrionomys* spp. and there should be a significant correlation between frequency of chitin and sand. Neither of these requirements was fulfilled in the present study. This does not disprove the possible function of sand, but suggests that its ingestion is accidental rather than intentional and is not likely to have a genetic basis. If sand ingestion is learned, the process must occur at an early age since no differences were found in consumption rates of sand by juveniles and adults.

Dietary restriction and nutritional wisdom. Only a small portion of the total primary productivity is used as food by consumers. In this respect Drożdż (1967) estimated that *Apodemus flavicollis* used 2.4 per cent of the net primary production and *C. glareolus* 4.4 per cent. Of the foods present in the environment, supply does not indicate availability, nor does consumption indicate requirements—because of the selective nature of the diets of animals.

In the wild selectivity has been shown by *Lemmus lemmus* (Stoddart, 1966), *C. glareolus* (Holišová, 1966), *Thomomys talpoides* (Ward and Keith, 1962; Myers and Vaughan, 1965; Vaughan, 1967; Tietzen *et al.*, 1967), *Microtus ochrogaster* (Fleharty and Olson, 1969), *Sigmodon hispidus* (Fleharty and Olson, *op. cit.*) and a host of others.

The factors which successively restrict food habits and nutrition



are as follows:

(1) *Availability*. Initially, the animal relies upon environmental resources and their seasonal accession. According to Sharpe (1965), *Microtus pennsylvanicus* in southern Alberta is a species in which availability is almost totally responsible for diet. The temporal and spatial effects of this basic factor have been seen in the current study. It is believed, for example, that fruits such as those of *A. rubra*, *V. oxycoccus* and *R. acaulis* are scarce in the diet because of their scarcity in the environment. Also, availability, not preference, explains the consumption of overwintered fruits.

(2) *Accessibility*. Availability refers to a potential which is usually diminished by environmental impediments (from the standpoint of the habitat) and morphological and behavioural shortcomings (from the standpoint of the animal). Among environmental impediments to feeding by the present subjects were melt water, snow cover, height of food above ground (e.g. fruits of *S. canadensis* and *C. stolonifera*) and thorny stems (e.g. fruits of *R. strigosus*, *R. woodsii* and *Ribes* spp.). Behavioural and morphological restrictions include the external body characteristics presented in Figure 1 and the activity phenomena discussed above.

(3) *Structural incompatibility*. The obtainable foods are, in turn, diminished in availability by barriers to ingestion and assimilation. Important among these determinants is *size* of food, especially in the case of animal foods and seeds. Kear (1960) reasoned that, other things being equal, finches will develop a preference for the largest seed they can efficiently manage, efficiency being measured in the weight of kernel extractable in a given length of time. Where an increase in the size of the seed taken leads to a drop in efficiency, a preference for a smaller





seed develops. In *P. maniculatus* of the present study, the highest fruit preference (Fig. 25) is for seeds of 2 mm length (Fig. 17) with decreasing preference for increasingly larger and smaller seeds. (*S. canadensis* has an unexpectedly low value.) These observations may, like those of Kear (1960), represent a preference for the largest seeds conveniently eaten whole; larger seeds requiring energy expenditure to break the coat, and the smaller seeds having little energy to offer. Thus, in *P. maniculatus* a selection may have been evolved or learned for seeds with the most energy value in relation to the energy required to consume them.

With the exception of the low preference for the fruits of *R. oxyacanthoides* and *S. canadensis* (tall plants with, possibly, inaccessible berries) the fruit preference of the vole (Fig. 25) increased with decreasing seed size. This decrease in seed size is concomitant with, generally, an increase in the proportion of flesh. A greater preference for flesh in *Clethrionomys* than in *Peromyscus* has already been suggested.

West (1960) suggested that *hardness of coat*, as well as large size, is the reason for seed exclusion in the diet of tree sparrows (*Spizella arborea*). *Food consistency* is another important determinant. For example, *P. maniculatus* of the Mackenzie area did not eat identifiable lichens most likely because of dental and alimentary incapacibilities (Fig. 1). Wood and heavily cuticled leaves were eaten less by all three cricetids in the laboratory than succulent plant parts, probably for the same reasons. *Digestive proficiency* for coarser foods was less for *Peromyscus* than for *Clethrionomys* spp. likely because of differences in alimentary apparatus (Fig. 1).

(4) *Preference*. That foods possess a differential "attraction" for





the animals of this study was demonstrated by the *passage* and *time* preference indices. Differential "palatability" was shown through the *weight* index. Thus, foods which may be accessible and compatible with ingestion and assimilation may have a low preference for some other reason. Examples of this situation in the present study were some fruits not accepted by any of the animals and many succulent vegetative parts by the voles. This factor, then, further diminishes the natural diet.

(5) *Nutritive value*. This factor may be interpreted as adding yet a further dietary restriction. Alternatively, it may be equated with preference. Which of these alternatives is the correct one is the answer to the question: do animals demonstrate "nutritional wisdom" (Albright, 1969) or, more popularly stated, do they eat what is good for them? Selection wisdom does not appear to exist in sheep (Gordon and Tribe, 1951; Arnold, 1962) and cattle (Albright, 1969), although beef and dairy calves show some wisdom in choosing milk composition (Hafez and Lineweaver, 1968). Crampton and Lloyd (1959) found no nutritional wisdom in young pigs, and Kare (1966) concluded that preference is generally not a reliable guide to nutrient value. In natural populations, Cowan, Hoar and Hatter (1950) suggest that palatability has nothing to do with nutritive quality in moose. Kalela (1957) found that all species of lichens offered to *C. rufocanus* were inferior as food, and yet Koshkina's (1957) animals of the same species ate great quantities of them. At the extreme, West's (1960) data show a negative selection for caloric content in tree sparrows (*Spizella arborea*).

On the other hand, although Scotter (1965) says that food preference in caribou (*Rangifer tarandus*) for various lichens "seems inconsistent



with the requirements of the animals," he does point out a preference for high fibre content (energy). Baumgardt (1969) thinks that "animals eat for calories." Nutritional wisdom is thought to exist in *C. glareolus* (Holišová, 1966) and *Bonasa umbellus* (Korschgen, 1966). In hares (*Lepus americanus*) Radwan and Campbell (1967) found that levels of glucose and fructose appeared to be responsible for the observed order of preference. Laboratory rats and Mongolian gerbils when allowed a self-selected diet, on the whole chose the nutritionally best foods (Harriman, 1969a and b). Laboratory rats prefer balanced protein diets (Harper, 1967).

Therefore, according to the inconsistencies of the literature, preference for nutritionally valuable foods is not a universal phenomenon. This is what would be expected if preference were genetically controlled in some animals and not in others, or if the degree of chromosomal inheritance varied. According to Kendeigh (1961) the relative significance of genetics and learning, on which the food preference of any species depends, has not been evaluated. This hiatus still exists.

Emlen (1968), in discussing predators, reasoned as follows: "Inasmuch as food preferences may be at least **partially** controlled by genetic factors, one would assume that natural selection has favoured those genotypes which predispose their owners to favour the 'right' foods, that is, those that yield the most in net energy and nutrients per time to their predators." This argument is sound assuming some degree of genetic control.

A review of the preference, consumption and nutrient values of the dietary components of the present animals ought to give some idea of their degree of nutritional wisdom. According to Crampton and Lloyd (1959) the balance between protein and calories is particularly important in





maintaining normal body tissues. Diets relatively high in calories but low in quality and quantity of protein cause depletion of protein reserves in the body. In my feeding tests (Tables 12 and 13) maintenance requirements were seldom met, probably because of protein shortage, causing tissue breakdown "commonly revealed by a loss of weight and which leads to various undesirable consequences" (Maynard and Loosli, 1956). As a rule of thumb for adult animals most natural foods that are primarily sources of carbohydrates (the dry matter of foods of herbivores is principally carbohydrate) carry one gram protein to every 35 to 50 kilocalories *metabolizable energy*. This is roughly equivalent to ten per cent of the kilocalories from protein (Crampton and Lloyd, 1959). Although little is known about the relative digestibility of the food species and their parts, mainly from these premises of Crampton and Lloyd (*op. cit.*) the maintenance values determined in the present investigations may now be interpreted and compared to preference.

Lichens are generally high in carbohydrate content and low in protein (Scotter, 1965) and the protein to calorie ratio decreases throughout the winter (Scotter, 1965; Short, Dietz and Rammenga, 1966). On these foods the animals did poorly except in the cases of the arboreal lichens which are not necessarily better foods than the ground lichens (*Peltigera* has relatively high protein value according to Scotter, 1965). High natural consumption by voles in winter is probably a matter of necessity and not necessarily preference.

Only mushrooms met the minimum maintenance requirements. Getz (1968b) concurs that this food is sufficient to maintain weight, at least in *C. gapperi*, for 44 days. Koshkina (1957) found that for *C. glareolus* only seeds and mushrooms were "full-value" foods. Although this food is low in





both energy content and protein, the protein to calorie ratio exceeds ten per cent (Chaney and Ross, 1966). A high preference index matches the high maintenance value of this food although it is not a significant part of the natural diet of *P. maniculatus*.

Stems are relatively low in protein, and their carbohydrates are mainly "roughage." Preference for and consumption of stems was generally low in all three species. Leaves which, together with stems, have a low fat content (Short, Dietz and Rammenga, 1966) but are rich in vitamins (Maynard and Loosli, 1956) have a relatively high protein to calorie ratio (Maynard and Loosli, *op. cit.*) and maintenance value but a relatively low preference. However, the more succulent leaves which are higher in protein content (Short, Dietz and Rammenga, *op. cit.*) are generally superior in both maintenance and preference. Perhaps the low protein content of narrow-leaved plants (Maynard and Loosli, *op. cit.*) explains the insignificant role of grasses in the diet.

The protein to calorie ratio of fruits is usually less than two per cent—far below requirements for maintenance, as the tests bore out. In fact, fruits are about the only natural food whose *dry* substance is really low in protein (Crampton and Lloyd, 1959). Also, as a general rule, foods such as fruits, which contain much water, are poor sources of energy (Chaney and Ross, 1966). However, these foods generally had high preference values which were reflected in natural consumption. Nevertheless, seeds are high in protein value (Westerskov, 1964)—higher at maturity than the rest of the plant (Maynard and Loosli, *op. cit.*).

According to Chaney and Ross (*op. cit.*) arthropods are low in energy and moderately high in protein (protein to calorie ratio, roughly 20 per cent). In fact, with the exception of milk, the absence of carbohydrates



in animals, as opposed to plants, is striking (Crampton and Lloyd, 1959). Arthropods are highly preferred and consumed by *P. maniculatus*.

Other nutritive components of foods may explain preferences and consumption of the Mackenzie cricetids. The high water content of fruits (according to the values of Chaney and Ross [1966] *F. virginiana* would approximate 90 per cent; *R. strigosus*, 84 per cent) although it dilutes nutrient value, provides a nutrient in itself and beneficially influences the intake and efficiency of other nutrients (Crampton and Lloyd, 1954). As suggested by Getz (1968b) succulent fruits in late summer afford an excellent water supply, and in the present case may explain the high preference of this food in terms of nutritive wisdom. Thus, the water content of various foods was found to be important in *Lepus californicus* (Hayden, 1966) and *Thomomys talpoides* (Vaughan, 1967). Getz (*op. cit.*) reported that even *C. gapperi*, which has relatively high water requirements, was capable of using mushrooms as sole water source in laboratory tests. Where water is limiting, the high consumption of mushrooms by voles could be explained by this constituent alone. However, in the preference tests water was supplied in excess and high values were still obtained for mushrooms.

Foods may also be consumed for micronutrients. For example, the high preference for fruits (Figs. 24, 25 and 27) may be explained through their relatively high concentrations of calcium, phosphorus (in seeds), ascorbic acid, thiamine, riboflavin and niacin (Chaney and Ross, 1966). But if calcium and vitamins were selected for, stems and more important, leaves, should have higher preferences (Maynard and Loosli, 1956; Short, Dietz and Rammenga, 1966).

Finally, the possibility of selection for nutritional balance in a





whole regime rather than individual components must be considered.

Energy and protein are complemented in the spring diet of overwintered fruits and new leaves in *Clethrionomys* spp. and of overwintered fruits and arthropods in *Peromyscus* (Figs. 29 and 30). Late summer and winter diets, however, are composed of foods high in energy and low in protein, while the environment offers a choice of a higher protein diet.

From the above it is safe to say that nutritive wisdom is not shown in all cases by the major cricetids of the Mackenzie area and, therefore, genetic control is probably absent or unimportant. It follows that any nutritionally favourable preferences are taught by the parents or learned by experience. Such learning must have taken place before trappable age since the data show no difference in consumption between juveniles and adults (Fig. 30). That consumption differences between age classes occur has been witnessed at least in gophers (*Thomomys talpoides*) by Myers and Vaughan (1965) and in dormice (*Dryomys nitedula*) by Kratochvíl (1963).

## Annual Fluctuations

Cycles. Although *fluctuations* may only be properly called *cycles* if they show regular amplitude and periodicity, the literature abounds with instances of "cyclic" temporal changes in natural populations (reviews in Elton, 1942; Dymond, 1947; Keith, 1963). These mystical oscillations may be illusions caused by data manipulations, mainly smoothing (Slobodkin, 1961) and indeed, may be random phenomena (Palmgren, 1949; Hutchinson and Deevey, 1949; Cole, 1951 and 1954). Considering the prevalent loose usage of the word, a bias in favour of the reality of cycles may exist. As Lack (1954a) remarked, "the human mind seeks for regularity in remarkable events."





If the cycles are real, they may be explained by the inherent dynamics of Volterra (1931) in very simple trophic relations or by reproductive potential (thus, the differences in period depending on size and reproductive rate) and negative feedback—the "inertia" of Koshkina (1966). The final possibility is the generation of such oscillations by regularly recurring events in the environment such as "seed years" (Laukhart, 1957; Adamovich, 1957), favorable winters (Fuller, Stebbins and Dyke, 1969) or the "fruit years" and "mushroom years" of the present study. These possibilities are not necessarily mutually exclusive.

Koskimies (1955) suggested that cyclic herbivores live on "vegetative capital" (stems, leaves), the production of which is dependent on the use made of the previous year's crop; and non-cyclic ones live on "vegetative interest" (reproductive parts), which production is independent of effects from the year before. Assuming numbers fluctuate with variations in these foods, a different hypothesis is necessary for the Mackenzie area as substantial annual variation took place in fruiting parts, whereas herbage and shrubbery production varied little. This different hypothesis was substantiated in my study in that both genera are reliant to a large extent on reproductive parts—*Peromyscus* on fruits and *Clethrionomys* on fruits and mushrooms—and both fluctuate, if not cycle (Fuller, 1969a). In addition voles, which depend more on vegetative foods (i.e. "capital"), were found to fluctuate less than mice, which depend more on reproductive parts (i.e. "interest"), (see also Fuller, 1969a).

Northern populations. Conspicuous numerical changes are particularly characteristic of northern regions. For example, in this study, and that of Fuller (1969a), *P. maniculatus* was seen to fluctuate in the taiga although southern races do not generally show regular numerical changes



(Terman, 1966; Jameson, 1955). The strong fluctuations of northern regions have been attributed to the simplicity of community structure with fewer checks and balances, that is, fewer alternatives of predators, food, etc. (Dymond, 1947; MacArthur, 1955; Hutchinson, 1959; Odum, 1959; Dunbar, 1960; older references in Lack, 1954a; but see Formozov, 1966). Thus, a specialized diet or lack of choice is more likely to subject the population to the vagaries of the biotic environment and, indeed, is blamed for the more commonly observed food destruction in cultivated and northern areas (review in Lack, 1954a). Of the present animals such a lack of flexibility is most characteristic of *P. maniculatus*.

Influence of food. Simple food relations of the types found in mathematical models are not likely to be found in nature at any latitude, and certainly not for organisms of the second trophic level. The present study indicates that, contrary to popular opinion, the choice of foods in the taiga is high and varied and no indication of foraging pressure on resources is noticeable. It is this high number of alternate foods and relative lack of food destruction (Hairston, Smith and Slobodkin, 1960; Slobodkin, 1961; Fleharty and Olson, 1969) that has cast doubt on the hypothesis of food limitation at the trophic level of the present subjects, although empirical evidence against the hypothesis also exists, for temperate populations at least (Górecki and Gębczyńska, 1962; Grodzinski, 1963). Food limitation, however, may be more subtle than denudation of vegetation or local extinction of prey. The phrase "relative shortage of food" was coined by Andrewartha and Birch (1954) to explain the paradox of scarcity amid plenty due to inaccessibility. I have attempted to demonstrate how the use of total productivity is restricted by several factors. Studies such as those of Grodzinski (1963) do not take the





influence of such factors into account.

Kalela (1957) suggested that intergroup selection should favor groups autoregulating their numbers below the food limit at critical periods. Although Malthus (1798) recognized proximate checks to population growth, he considered food the ultimate one. Recently, Wynne-Edwards (1962) recognized food as a possible ultimate factor, but not a proximate one. Even Lack (1966) claims that herbivorous mammals, at least, never reach the limit to density imposed by food. Elton (1927), Kalela (1954), Tinbergen (1954), Koskimies (1955), Andrewartha (1961), Slobodkin (1961) and Klopfer (1962) also agreed that numbers are maintained below the level at which food becomes limiting. Evidence from laboratory (Strecker and Emlen, 1953; Terman, 1965) and field (Krebs, 1963; Chitty, Pimentel and Krebs, 1968) studies on various rodents also suggest this. On the contrary many authors hold that food proximally limits numbers (e.g. Grinnel, 1904; Braestrup, 1940; Lack, 1954 $\alpha$ ; Lauckhart, 1957; MacArthur and Connell, 1966).

That populations sometimes reach the limit set by food supply is verified by some well-documented cases which occur mainly in (1) animals which increase their numbers excessively such as *Microtus* (Piper, 1909; Siegler, 1937; Elton, 1927; Charles, 1956; Hoffmann, 1958; Spencer, 1958; Mueggler, 1967) and lemmings (Elton, 1924; Thompson, 1955; see also Elton, 1942 and F. Frank, 1957); (2) animals whose predators have been artificially eliminated (Rasmussen, 1941; Leopold, 1943; Ball and Hayne, 1952; summary by DeBach, 1958); and (3) animals introduced into regions where factors which would otherwise control numbers are absent (Nicholson, 1947; summary by Elton, 1958).

Other instances of food influence have been recorded for such animals





as wolves (Murie, 1934), great tits (Lack, 1966), grey squirrels (Seton, 1920; Goodrum, 1940; Sharp, 1959; Smith and Barkalow, 1967; Nixon and McClain, 1969), red squirrels (Formozov, 1933), fox squirrels (Allen, 1954), white foxes (Chitty, 1950), snowy owls (Chitty, 1950), and house mice (Evans, 1949). "Seed years" are correlated with fluctuations in tropical (Troupe, 1921) and temperate (Górecki and Gębczyńska, 1962) regions as well as northern ones (Lauckhart, 1957). Some bird populations are more dense where their prey is more plentiful (Murphy, 1936; Lack, 1954b; Wynne-Edwards, 1962) and raise larger (Rendall, 1925) or more (Schmaus, 1938) broods.

Holišová (1966) discounted the food hypothesis for *C. glareolus* numbers in Czechoslovakia. However, Koshkina (1957) supported the hypothesis for both *C. glareolus* and *C. rutilus* on the Kola Peninsula; but she suggested that *C. rufocanus*, which lives mainly on greens, is less subject to environmental vicissitudes. Note that her hypothesis is directly opposite to that of Koskimies (1955). Koshkina (*op. cit.*) reviewed Bashenina (1947, 1951) and Formozov (1948) who found in certain "seed years" that reproduction of *C. glareolus*, and especially of *C. rutilus*, was protracted into late fall and resumed in early spring under the snow. In the current study, no such protraction and early resumption took place after the "fruit year" of 1966.

*P. maniculatus* numbers, at least in temperate America, may be changed by both animal (Holling, 1959) and vegetable (Linduska, 1942) foods. The present data, however, do not directly support the food hypothesis for that species.

That increased quantity or quality of food may increase the reproductive rate has been shown in several laboratory tests (e.g. Bodenheimer,



1949; Pinter and Negus, 1965; Stodart and Myers, 1966), and in the wild for lions (Stevenson-Hamilton, 1937), arctic foxes (Braestrup, 1941), wapiti (Cowan, 1950), and white-tailed deer (Morton and Cheatum, 1946). Conversely, the birth-rate of sheep blowflies (Ullyett, 1950; Nicholson, 1954), *Daphnia* (Berg, 1931; Brooks, 1946; Slobodkin, 1954), copepods (Hutchinson, 1951) and humans (Kuczynski, 1936; Lack, 1954a) decrease in times of famine.

The importance of food in reproduction is attested to by the fact that, in nature, the sexual cycle is timed so that pregnancy and lactation coincide with the seasons when food is most abundant. Nutritional requirements are higher for reproducing adults than for non-breeding animals (reviews in Maynard and Loosli, 1956; Crampton and Lloyd, 1959; Chaney and Ross, 1966; Hafez and Dyer, 1969). Particularly in temperate and boreal rodents in spring nutritional demands are critical because of the additional burden of weight increase (Stebbins, 1968).

Overwintered females of the three rodent species of the present study give birth to their first litters in late May, and the second around the end of June or the beginning of July. Third litters are born to *Clethrionomys* in late July-early August, but fourth litters, like the third of *Peromyscus*, are probably unimportant contributors to population density (Fuller, 1969a). In each species some females of the first litter may become sexually mature before the end of the breeding season, and bear one or two litters of their own.

Therefore, nutrition is of particular importance for the reproductive females during the production of the first two litters (the "vernal" period of the present study) which exert the greatest influence in summer population recruitment. Judging from stomach volumes (Fig. 30) females





may eat more than males in spring; and both sexes eat more in spring than they do later in the season. Thus, quantitative and qualitative variation in spring nutrition may have far-reaching consequences, especially for females. Grodziński and Górecki (1967), for example, assume that, in small rodents, energy requirements of reproductive females increase by over one-half.

For the current study the decrease in total adult stomach volume from May throughout the summer (Fig. 30) may be due to: (1) decreased reproductive requirements as summer progresses; (2) the population becoming increasingly younger with increasingly smaller stomach capacities; or (3) increasing density causing increased competition and/or interactions. However, even stomachs of juveniles at trappable age, were of great volume (Fig. 30), making the second explanation questionable. An apparent inverse relationship between density (Fig. 37) and total stomach volume (Table 16), perhaps a result of competition for limited resources at high numbers, gives support to the third explanation.

New green shoots and leaves, high in protein (Maynard and Loosli, 1956; Short, Dietz and Rammenga, 1966) appear to influence reproductive rate positively in *Microtus californicus* (Hoffmann, 1958) and *M. montanus* (Hoffmann, 1958; Pinter and Negus, 1965). The latter suspect the active ingredient in such foods may be "plant estrogens." Chitty (1960) mentions an annual shortage of green material in the year of decline of *M. agrestis* in Britain, but Baker and Ranson (1933) found no influence of green material on the same species in the laboratory.

*P. maniculatus* of the present study, because of insect consumption, may be expected to be free of the influences of green foods in spring; but *Clethrionomys* may depend on such foods. The delayed phenology and





less vigorous plant growth of 1967 did not noticeably alter the chlorophyllous diet of *Clethrionomys* spp. quantitatively, and may not be directly implicated in the reproductive slowdown and delayed weight gain at that time in *C. gapperi* (Fuller, 1969a). However, it is possible that 1967 was characterized by greater expenditures of energy and greater intraspecific strife to make up for the relative unavailability of chlorophyllous material in that spring.

Food in the present populations probably played its major role in the spring of 1968 when overwintered fruits were much scarcer than in any of the other springs. At that time insects were a nutritious alternative for *P. maniculatus* but the alternatives to these fruits for *Clethrionomys* spp. were lichens, whose scanty protein content had declined throughout the winter (Scotter, 1965), and leaves and stems which were little eaten in the earliest part of spring. Naumov (1934) found that squirrels eating coarse foods such as arboreal lichens rapidly lost weight (see also Tables 12 and 13) and propagated poorly.

In a more general sense, the diets of the animals in the current study reflected annual changes in phenology and availability with some sensitivity. Therefore, it is possible that food supply may at least have influenced the "magnitude and pattern" (Murray, 1965) of numbers if it did not instigate the changes. For example, the stronger fluctuations in *P. maniculatus* than in *Clethrionomys* (Fig. 37; Fuller, 1969a) may be owing to their total dependence on fruits during summer (Fig. 31) regardless of whether climatic conditions dictate a "fruit year" or "mushroom year."

Weather and food. Darwin (1859) submitted that indirect influence of weather through food is more important than its direct influence on



animals. Weather has been seen by many workers (e.g. Braestrup, 1940; Ward and Keith, 1962; Kalela, 1962; Nixon and McClain, 1969) to affect vegetation qualitatively or quantitatively. The current study has also demonstrated a correlation between weather, phenology and production. That weather may thus influence numbers—especially of rodents—indirectly through food has been suggested many times (Braestrup, 1940; Bodenheimer, 1949; Lauckhart, 1957; Orians and Pitelka, 1960; Kendeigh, 1961; Negus and Pinter, 1966; Nixon and McClain, 1969) and is suggested in the present study through its influence on the important overwintered fruits, which influence is extended from one year to the next. It is conceivable, indeed, that synchrony in fluctuations (Elton, 1924; Koshkina, 1966) may not necessarily be only directly due to weather but also to its influence on the food supply.

Taiga is probably more notable for its climatic extremes and snow-cover (Formozov, 1946; Fuller, Stebbins and Dyke, 1969) than for its trophic simplicity. This is especially true for the animals of the present work which have a high surface:volume ratio, and which are subject to periods of potential thermal stress at times when food is scarcest, and needed for both reproduction and recovery of winter weight loss. Since much more food is needed to maintain those requirements, as well as body temperature, at lower ambient temperatures (Dice, 1922; Rowan, 1925; Westerskov, 1964) climate and food should not be considered independently in northern regions. Thus, although climate appeared to have played a *minor* role in the population decline of 1968, it played a *major* part in 1967 but not without nutritional inferences. Thermal stress (Fuller, 1969a) is assumed to have caused reproductive slowdown and lack of weight gain in *P. maniculatus* and *C. gapperi* in 1967; but the food required to maintain





body temperature during such stress may have become limiting, a phenomenon which Howard (1949, 1951) called "cold weather starvation." In that spring (1967) the stomach contents of *C. rutilus* were of much larger total volumes (Table 16) than those of the other two species so that *C. rutilus* may have escaped the fate of *P. maniculatus* and *C. gapperi* (Fig. 37) by thwarting "cold weather starvation" through a greater ability at overcoming the obstacles to accessibility—snow cover and standing water—which were most severe during the spring of 1967. If this was the case, the extraordinary crop of overwintered fruits in the winter of 1966-67 could only have had a beneficial effect on *C. rutilus* (Fig. 31). In addition, the reduced habitat (because of snow and water) of *P. maniculatus* and *C. gapperi* may have increased density causing reproductive failure (Fuller, 1969a) through "intraspecific strife" (Canham, 1969). This explanation best suits *P. maniculatus* which consumed great quantities of insects as well as overwintered fruits in the spring of 1967. As was noted earlier, there was a delay in appearance of leaves and a less vigorous growth of vegetation in 1967, making "nutritive-through-thermal" stress, as well as social stress, more acute.

The greater survival rate of *Clethrionomys* in the winter of 1966-67 than in the winter of 1965-66 (Fuller, Stebbins and Dyke, 1969) is correlated with a greater consumption of overwintering fruits of *V. vitis-idaea* (Fig. 32) together with higher subnivean temperatures (Fuller, Stebbins and Dyke, *op. cit.*).

Population dynamics. Apparent causes of density changes in the current populations represent a single set of phenomena of which, judging from the literature, there must be countless combinations affecting numbers throughout the biosphere. Nevertheless, some principles of population





ecology exist, which are basic to the several schools of number explanation.

Temporally, as well as spatially, populations exert a "pressure" and but for "environmental resistance" (Chapman, 1928) would expand in time and space. This happens in fact, when all, or nearly all, environmental conditions happen to become favourable at once (Thompson, 1929), as happened prior to, and during, 1966 of the current study. Resultant exceeding of the "optimum density" (Burov, 1968) (*per se* or with respect to environmental resources) from this inherent capacity to increase may be alleviated either by a further amelioration of the environment or by a reduction in increase in population. The second alternative is ultimately inevitable, and may be proximally effected through the following means, singly or in combination.

(1) *Reproductive failure* (Crew and Mirskaia, 1931; Pearl, 1932; Prat, 1943; Errington, 1946, 1951; Harris, 1956; Patric, 1962; Keller, 1968 and a multitude of others) may be the most common check, and is the one implicated in the present study.

(2) *Mortality* (Elton, 1927; Lack, 1948; Hoffman, 1958; Koshkina, 1966; Pearson, 1966 and others) is reported less frequently in the literature, perhaps because of the difficulty of direct documentation.

(3) *Emigration*, to be examined in a later section.

These checks, the reverses of which cause numerical increases, are, of course, the mediators of more fundamental causes which comprise the controversial aspect of population dynamics. Such causes, for any given population, may not necessarily be totally environmental, e.g. the trophic (Cowan, 1950; Strecker and Emlen, 1953; Pitelka, 1958) and climatic (Uvarov, 1931; Fuller, 1969a) causes discussed in the present work. The demographic data of Leslie and Ranson (1940) and Negus and Pinter (1965) for *Microtus*



suggest that, in these animals at least, at high populations more young adults are present which give birth to smaller litters, thus slowing the rate of increase of the population. An intrinsic mechanism is also implied in data for *C. gapperi* (Patric, 1962), *C. rutilus* (Koshkina, 1957 and 1966), *C. rufocanus* (Kalela, 1957; Koshkina, 1957 and 1966), *Microtus* (Frank, 1953; Clarke, 1955; Krebs, 1966), *Rattus norvegicus* (Davis, 1951), *Mus musculus* (Crowcroft and Rowe, 1957; Rowe, Taylor and Chudley, 1964), *Ondatra zibethicus* (Errington, 1946 and 1951) and, among the invertebrates, for *Hyallela* (Wilder, 1940) and *Daphnia* (Prat, 1943).

Territoriality enables the maintenance of optimum densities, or "regulation" of numbers (Elton, 1927, Klopfer, 1962), but there is doubt as to whether it does (Stickel, 1968) or does not (Blair, 1953) exist in cricetids. If it does, the case for direct food effect on temporal numbers would be weakened. However, according to Southwick (1955*b*), F. Frank (1957), Stickel (1968) and Elliott (1969) these animals may condense their distribution during periods of high numbers necessitating checks such as social stress (Crew and Mirskaia, 1931; Clarke, 1955; Selye, 1955; Southwick, 1955*a* and *b*; Harris, 1956; Kalela, 1957; Crowcroft and Rowe, 1959; Canham, 1969) and endocrine anomalies (Christian, 1950; Christian and Davis, 1956; Helmreich, 1960). Such checks may come into play at extreme numbers but are not likely during such "weak peaks" (Fuller, 1969*a*) as those of the present study. However, the nutritive stress (Cowan, 1950 and Andrewartha, 1961) postulated in the present study for *C. gapperi* in 1967 as *nutritive-through-thermal* stress, may have caused reproductive failure through endocrine anomalies and/or social stress (Canham, 1969). Christian and Davis (1956) regard such anomalies to occur through complex combinations of





social and nutritive factors. Change in the genetic make-up of the animals (Chitty, 1960; MacArthur and Connell, 1966) does not seem to be required to explain the observations of the current study.

### Biotopic Densities

Distribution is probably determined by the environment as a whole and should reflect the total physiological and ethological requirements of the animal as well as the structure of the community. Thus, Johnson (1926) believed the whole "biotopic association type," rather than any single factor of the environment, to be of primary importance in the distribution of wild mice. Although the "real" habitat (Elton, 1927) must be defined in terms of a synthesis of limiting factors only a few disconnected factors can be discussed here.

Factors influencing spatial density. Water may limit distribution, especially during pregnancy and parturition (Lindeborg, 1950) and at times of high activity (Chaney and Ross, 1966). Moisture restricts the distribution of *C. gapperi* in Virginia (Odum, 1944) and standing water is an environmental requirement for the same species in New England (Getz, 1967 and 1968b). Although the voles of the current study showed no specific moisture restrictions, like *C. rufocanus* (Kalela, 1957) they were not plentiful in the driest areas (jackpine forests) or in those with standing water (immature black spruce forests, especially tamarack fens). *P. maniculatus*, whose water requirements are much lower (Dice, 1922; Odum, 1944; Getz, 1967 and 1968b; Table 15), is not likely to be positively dependent on moisture or standing water. In fact, it was found in dry areas in the present study as well as in those of Linduska (1942), Odum (1944), Getz (1967) and many others. Generally, the three basic vegetation types—black spruce, white spruce-poplar, and jackpine, in increasing





order of dryness—harbour voles in the wettest habitats and mice in the driest (Fig. 38).

Because of relative opportunism in *Clethrionomys* and mobility in *Peromyscus* food availability is not a likely candidate for explanation of spatial densities. A suggestion of the dependency of spatial numbers on food was the predominance of *P. maniculatus* on edges of forests where live-traps were usually set to catch experimental mice, and where the highly preferred and consumed fruits of *R. strigosus* and *F. virginiana* were by far the most plentiful. This was also the only place where the highly preferred leaves of young *P. tremuloides* were found. The general association of voles with black spruce, mice with jackpine, and both genera with white spruce-poplar is also remarkable since these community types were deduced from floristic (i.e. food) composition only. As seen in Table 17, however, fruit preference does not predict habitat selection. Evidence of food influence on the spatial densities of small herbivores is also lacking in the literature.

The high correlation between density and foliage cover (Fig. 39) indicates that cover may be the most important environmental variable for *Clethrionomys*. *C. gapperi* shows such a correlation in Alberta (Dyke, 1970) as does *C. rutilus* (Steven, 1955), *C. glareolus* (Prof. K.R. Ashby, *pers. comm.*), *Microtus pennsylvanicus* (Beckwith, 1954; Jones, 1964; Root and Pearson, 1964; Sharp, 1965), *Neotoma fuscipes* (Vogl, 1967), *Ondatra zibethicus* (Errington, 1946) and *Sigmodon* (Goertz, 1964b). It may be that cover is a major factor of carrying capacity in the habitats of small, secretive herbivores of the taiga as has been well documented for more southerly latitudes.



*P. maniculatus*, however, shows a low correlation with foliage cover (Fig. 39) as reported in the literature for Alberta (Sharp, 1965; Dyke, 1970), as well as for more temperate latitudes (McCabe and Blanchard, 1950; Beckwith, 1954; Kendeigh, 1961; Whitaker, 1966 and 1967a; Baker, 1968). Whitaker (1968) gave as a reason the loose soil, suitable for burrowing, in areas of low cover. That *P. maniculatus* is primarily nocturnal (Stebbins, 1968) may be partly responsible in the present case.

The high correlation of deermouse numbers and the frequency of fallen trees (Fig. 39) is confused by the fortuitous high correlation between fallen trees and litter ( $r=0.75$ ). Thus, the correlation coefficient for litter and mouse density is  $+0.77$ , almost as high as for fallen trees. However, considering the qualitative as well as the quantitative aspects of litter the magnitude of the coefficient is exaggerated insofar as this factor may be interpreted as *shelter*. It is possible that *P. maniculatus*, being carnivorous, seeks out these sites for nutritional reasons because of the high numbers of invertebrate detritus feeders in sites with a high aspen leaf litter (La Roi, 1967). But most of the sites had litters of unpalatable coniferous needles. The value of litter is lowered after partial correlation while that of fallen trees (and foliage cover in *Clethrionomys*) is raised (Table 17).

Few reports of the significance of fallen trees could be found in the literature. Olszewski (1968) suggests that *Apodemus flavicollis* used the upper surfaces as convenient routes through the forest. Root and Pearson (1964) who found *P. leucopus* associated with the same factor, give the same explanation. Although none of my animals were seen in nature using the upper surfaces of logs as pathways, those released from





live-traps often used them for quick escape, an observation also made by Root and Pearson (1964).

Interspecific relations. Interspecific competition has been postulated mathematically (Lotka, 1925; Volterra, 1931), and produced experimentally (Gause, 1934; Crombie, 1947; Park, 1948; P.W. Frank, 1957; Birch, 1953). Unfortunately, because we lack empirical evidence, its importance in determining natural density patterns is not really certain (F. Frank, 1957; DeLong, 1967; Park, 1962; MacArthur and Connell, 1966), notwithstanding the excellent studies of some workers (e.g. Lack, 1942; Wasilewski, 1967). Theorists ascribe little (Andrewartha, 1961), moderate (Soloman, 1949; Odum, 1959) and great (MacArthur, 1957; Hairston, 1959; Slobodkin, 1961) importance to this factor.

The data of the present work give circumstantial evidence of interspecific competition similar to that suggested by the studies of Cameron (1964), Clough (1964) and Morris (1969) between *Microtus pennsylvanicus* and *C. gapperi*; of Caldwell and Gentry (1965) between *P. polionotus* and *Mus musculus*; and of Sheppe (1967) between *P. maniculatus* and *Mus musculus*.

Sites are arranged in Figure 36 in order of the severity of the apparent vole displacement by mice in mid-summer. Such "displacement" does not bear any obvious relationship to preference (Figs. 24, 25 and 27) or consumption (Fig. 33) of spatially variable foods (Appendix IV). Of the cover aspects, "displacement" is correlated most highly ( $r=0.90$ ) with fallen trees, although litter ( $r=0.82$ ) is also high. (Partial correlation coefficients are 0.73 and 0.68 respectively.) Similar population dynamics were not reported by others working in the area (Stebbins, 1968; Meunier, 1969; Fuller, 1969a; Canham, 1969), and there is some





possibility of it being an artificial one. If this is not the case I suggest that voles may displace mice in winter when the latter are in torpor, and Figure 36 shows the culmination of the reclamation of those areas by mice in July when their numbers were highest (see also Pruitt, 1959). The voles, which attain their highest densities in August, start immediately a "winter encroachment" of the favored sites of the deermice (those containing fallen trees).

The effects of year-to-year population changes on cricetid composition of the biotopes (Fig. 40) are best explained by *Peromyscus* dependency on fallen trees (Fig. 39) and an assumed dominance over *Clethrionomys*, at least in summer. Thus, the *P. maniculatus* "peak" in 1966 displaced *C. rutilus* from the various sites with a severity depending on the fallen tree frequency (Table 9). When *C. rutilus* peaked in the following year (while *P. maniculatus* was declining), it increased in the three communities with highest fallen tree frequencies (Table 9), but to an extent reciprocally dependent on their frequency. The dramatic increase of *C. rutilus* in the mature black spruce stand in 1967 may be attributed to the ideal compromise the site offered the vole between its own requirements (foliage cover) and the lack of those of the more demanding *P. maniculatus*. These dynamics were not seen in *C. gapperi* territory possibly because of the simultaneous population peaks or the low numbers of fallen trees. Such an explanation of spatial numbers carries the further implication that, at high densities, *interspecific* as well as *intraspecific* stress (Canham, 1969) comes into play, and falls more heavily on *Clethrionomys*.

The population of *P. maniculatus* in *C. rutilus* territory was higher than that sympatric with *C. gapperi*. This was true in all the years of the study (Fig. 37; see also Fuller, 1969a); and for all biotopes



studied (Fig. 38). The three most obvious factors to explain this discrepancy are: (1) number of fallen trees, (2) food availability and (3) competition for food or some other factor between *P. maniculatus* and *C. gapperi* keeping numbers of mice in *C. gapperi* territory generally low and causing simultaneous peaks in 1966. The data of the present study can support either of the first two explanations (Tables 7 and 9) but cannot test the third hypothesis.

Although Stebbins' (1968) circadian rhythms did not indicate a proximal barrier to sympatry in the two species of *Clethrionomys*, the distal factors of food and cover, investigated here, indicate niche requirements so similar as to suggest competitive exclusion (Grinnel, 1904; Volterra, 1926; Lotka, 1932; Gause, 1934) as the reason for the marked separation of *C. rutilus* and *C. gapperi* on the study area. Note that Rand (1944) also found a fairly sharp boundary between these species on the Alaska Highway.

### General Considerations

Population ecology may be considered as an approach to community (Lindeman, 1942; Park, 1946; Hairston, 1959) or ecosystem (Allee, 1934; Tansley, 1935; Evans, 1956) ecology, or as an end in itself. Andrewartha and Birch (1954), in the spirit of Elton (1927), formulated a theory of ecology centered on the *population*. In fact, Andrewartha (1961) defined animal ecology as "the scientific study of the distribution and abundance of animals." The present work in population ecology is a study of the numbers of three rodents together with some possible influential environmental factors.

Although environmental components responsible for variations may



operate both *temporally* and *spatially* (Andrewartha and Birch, 1954), no support for such a 4-dimensional concept was shown by vegetation in the present study. Thus, although food may have some *temporal* significance it does not have obvious *spatial* significance: cover aspects of vegetation, on the contrary, appear to be influential *spatially* but not *temporally*.

The idea that weather influences annual fluctuations in arctic small rodents through its effects on primary production (Kalela, 1962) has received some support in this study. Variation correlated with differential weather conditions was seen in the production and consumption of the few important plant foods (fruits and mushrooms in *Clethrionomys* spp., fruits in *P. maniculatus*), and was especially noticeable in the important overwintered fruits in spring. Direct influence of weather on these populations has already been suggested (Fuller, 1969a).

The spatial correlates of density (fallen trees in *P. maniculatus*; foliage cover in *Clethrionomys* spp.) may impose ceilings to number increase (carrying capacity) beyond which intraspecific (Canham, 1969) and interspecific (this study) interactions cause "escape in space" (Slobodkin, 1961) or the emigration of physical and social inferiors to more marginal habitats where mortality is more likely (Kalabukhov, 1935; Errington, 1946; Koshkina, 1957; others). Such a mechanism, which would explain the dynamics of Figures 36 and 40, would act to prevent strong peaks or to dampen "cycles."

Like many others, then, this study requires more than a single-factor explanation of numbers.







## SUMMARY

1. During the four-year period the study area in the boreal forest of southern Mackenzie produced a large fruit crop in 1966, followed by relatively small ones in 1967 and 1968. These observations are explained by the climatically favorable springs of 1965 and 1966 as opposed to those of 1967 and 1968 which were characterized by low temperatures and persisting snow covers. Thus, primordia of 1965 were allowed to develop in 1966, but those of 1966 were inhibited in 1967. The 1967 primordia were, in turn, inhibited in 1968. Phenological delays in the last two years were also probably caused by the late springs. A large mushroom crop in 1967, and a slightly smaller one in 1968, were probably caused by summer months which were wetter than normal.
2. Stomach content analyses and food preference tests revealed that both *Peromyscus maniculatus* and *Clethrionomys* spp. are frugivorous and eat large quantities of a limited number of fruits. Fruits that overwinter on the plant are important in winter and early summer when the ephemeral ones are not available. In addition, *P. maniculatus* was found to be partly insectivorous whereas *Clethrionomys* spp. ate large quantities of mushrooms, chlorophyllous material and arboreal lichens. A similarity of trophic niche is seen for *C. rutilus* and *C. gapperi*. Mushrooms were found to be the only food to maintain body weight in all three species.
3. Annually, stomach contents faithfully reflected phenology. In low "fruit years" and high "mushroom years," which may have a common climatic cause, voles seem to have the ability to switch from fruits to mushrooms, whereas mice make up the lack by consuming the little-preferred overwintering fruits. Similar opportunism was shown biotopically in voles,



while mobility seemed to serve the food needs of mice.

4. The numbers of the three rodents increased in 1966, but in 1967, while *C. rutilus* continued to increase, *P. maniculatus* and *C. gapperi* declined. All species declined in 1968. The large fruit crop of 1966 provided an abundance of overwintered fruits in the spring of 1967 but, according to consumption and number increase, these appeared to benefit only *C. rutilus* in that summer. It is postulated that *C. rutilus*, unlike the other species, is able to thwart "cold weather starvation" through a greater ability to overcome obstacles to accessibility—snow cover and standing water—which were most severe in that spring. The decline in all populations in 1967-68 may have been abetted by the scarcity of overwintered fruits in the spring of 1968 following the poor crop produced in the cold wet summer of 1967.

5. Plant associations showed characteristic cricetid compositions best correlated with cover. *P. maniculatus* was associated with fallen trees, the surfaces of which may serve as easy routes through the forest. *Clethrionomys* was associated with foliage cover, which probably serves as shelter. Seasonal and yearly variation in faunal composition of the communities may be explained by dominance of *P. maniculatus* in interspecific interactions over habitat requirements. Similarity of food and cover niche requirements as brought out in this study may explain separation of the ranges of *C. rutilus* and *C. gapperi*.



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## A P P E N D I C E S



## APPENDIX I

## COMMON NAMES OF PLANTS



The following is a list, in alphabetical order, of the scientific names of all species of plants mentioned in the text, followed by their common names.

- Alectoria jubata* - an arboreal lichen
- Amelanchier alnifolia* - saskatoon-berry; service-berry
- Andromeda polifolia* - bog rosemary
- Arctostaphylos rubra* - alpine bearberry
- Arctostaphylos uva-ursi* - common bearberry; kinnikinnick
- Betula glandulosa* - dwarf birch
- Bryopogon* - an arboreal lichen similar to *Usnea*
- Calamagrostis inexpansa* - northern reed grass
- Calypso bulbosa* - Venus'-slipper
- Campanula rotundifolia* - harebell; bluebell
- Cetraria* sp. - a fruticose ground lichen
- Chamaedaphne calyculata* - leather-leaf
- Cladonia* spp. - reindeer moss
- Cornus canadensis* - bunchberry
- Drosera rotundifolia* - sundew
- Empetrum nigrum* - crowberry
- Epilobium angustifolium* - fireweed; great willow-herb
- Equisetum arvense* - common or field horsetail
- Equisetum scirpoides* - horsetail
- Eriophorum* sp. - cotton grass
- Fragaria virginiana* - wild strawberry
- Gallium boreale* - northern bedstraw
- Geocaulon lividum* - bastard toad-flax
- Habenaria* spp. - bog orchid





- Hydnellum* sp. - a mushroom
- Hylocomium splendens* - feather moss
- Juniperus communis* - ground juniper
- Juniperus horizontalis* - creeping juniper
- Larix laricina* - tamarack
- Lathyrus ochroleucus* - vetchling; pea vine
- Ledum decumbens* - northern labrador tea
- Ledum groenlandicum* - common labrador tea
- Linnaea borealis* - twin-flower
- Mitella nuda* - bishop's cap; mitrewort
- Moneses uniflora* - one-flowered wintergreen
- Parmelia* sp. - a foliose arboreal lichen
- Peltigera* spp. - a foliose ground lichen
- Picea glauca* - white spruce
- P. mariana* - black spruce
- Pinguicula vulgaris* - common butterwort
- Pinus banksiana* - jackpine
- Populus tremuloides* - aspen poplar
- Potentilla fruticosa* - shrubby cinquefoil
- Pyrola asarifolia* - common pink wintergreen
- Pyrola secunda* - one-sided wintergreen
- Ribes oxycanthoides* - wild gooseberry
- Ribes triste* - wild red currant
- Rosa woodsii* - common wild rose
- Rubus acaulis* - dwarf raspberry
- Rubus chamaemorus* - cloudberry; baked-apple berry
- Rubus strigosus* - wild red raspberry



*Russula* sp. - red-capped mushroom

*Sarcodon* sp. - a mushroom

*Shepherdia canadensis* - Canadian buffalo-berry

*Sphagnum* spp. - peat moss

*Spiranthes romanzoffiana* - ladies' tresses

*Vaccinium oxycoccus* - small bog cranberry; also known as

*Oxycoccus microcarpus*

*Vaccinium vitis-idaea* - bog cranberry; cow-berry

*Usnea* sp. - old man's beard; maiden hair

*Virburnum edule* - low-bush cranberry; mooseberry

*Vicia americana* - wild vetch



## APPENDIX II

### DIAGNOSTIC CLUES





The following list describes the diagnostic aids used in identifying the various foods found among the stomach contents of *P. maniculatus*, *C. rutilus* and *C. gapperi*. Within each major category the species are arranged in alphabetical order.

#### Arthropods (Fig. 17v)

Small arthropods occurred whole. Otherwise, chitinous fragments, whole appendages (legs, antennae) and eggs were found.

#### Mushrooms

Mushrooms usually appeared in the form of an opaque, rubber-like mass of various colors which conformed to the shape of the stomach.

#### Arboreal Lichens

*Alectoria jubata* (Fig. 17a). This food appeared as small dark smooth-surfaced threads with many branches. A dark inner thread could be seen traversing the diaphanous outer one. It differed from *Usnea* sp. in that it was broken into shorter pieces, was darker, had a more even outline, and the inner core never protruded, as in the former.

*Parmelia* spp. This brownish-colored lichen appeared in the form of smooth-surfaced curved pieces.

*Usnea* sp. (Fig. 17n). This light-colored food consisted of large branched cylinders, highly wrinkled and bearing many short protuberances. A smaller, smooth-surfaced inner core often protruded from the outer one.

#### Bryophytes

*Hylocomium splendens* (and perhaps others) (Fig. 17m). Tiny, finely dissected quantities of faint green "leaves" with a "fingerprint" design were the characteristics used to identify this plant.

#### Achlorophyllous Parts

These were nondescript except for the presence of tracheids and vessels.

#### Leaves

*Arctostaphylos uva-ursi* (Fig. 17p). The dark, thick, waxy leaf with deep, coarse venation (which appeared opaque), had closely-spaced hairs on the margin.

Conifer "needles". Microscopically these needles were thick and fusiform. They often occurred as fragments larger than those of *Empetrum nigrum* "needles", which were otherwise similar in appearance.



*Empetrum nigrum* (Fig. 17t). These "needles", smooth in outline and fusiform in shape, were often found whole. They were smaller than the similar conifer needles.

*Fragaria virginiana* (Fig. 17u). The finest veins of these leaves characteristically consisted of a single dichotomy. There were long, fine, closely-spaced hairs on the leaf edges and undersides where they grew mainly on larger veins. The pubescence here was shorter than that of *A. uva-ursi*.

*Geocaulon lividum* (Fig. 17r). This plant had the most coarsely venated leaves. The finer veins of this species lacked branches. Other characteristics which made this plant distinctive were the red veins on a brilliant green background and the lack of pubescence.

*Linnaea borealis* (Fig. 17s). The following characteristics were used to identify this plant: relatively thick leaf edge; indistinct venation; short, heavy, stiff hairs on the leaf edge; the most sparsely spaced of the leaf pubescences.

*Populus tremuloides* (Fig. 17q). The aspen leaf was the most finely-venated of the leaves studied. The smallest veins were intricately branched and the background was dark greenish-brown. Very fine hairs occurred on the edge of the leaf.

*Rosa woodsii*. Leaf veins were spaced in this plant as much as in *F. virginiana* but were more clearly outlined. Tiny dark papillae or "bulbs" were visible on the undersurface of the leaf. Also, relatively fine hairs were observed on the edge and undersurface of the leaf, particularly along the mid-line.

*Shepherdia canadensis*. The leaf appeared deep green with a silvery undersurface and a dense covering of hair. Tiny stellate appendages (as shown for the berry skin in Fig. 17k) always accompanied the leaf fragments, usually floating freely in the petri dish.

## Fruits

*Arctostaphylos rubra*. The red mass of the drupe was not diagnostic. The nutlet, with its orange, roughly-surfaced testa, through which a yellow embryo was visible, was used as a diagnostic trait.

*A. uva-ursi*. The large (2.5 mm) "seed" (united nutlet) was not eaten whole, and the fragments were not identifiable. Large cells which give the drupe its characteristic "mealy" texture were easily seen and were diagnostic.

*Cornus canadensis*. The red drupe mass of this fruit was not diagnostic. The stones (Fig. 17h) were characteristically pear-shaped.

*Fragaria virginiana*. The fruit pulp, which appeared dark among the stomach contents, only resembled that of *R. strigosus*. Achenes had characteristic branching and anastomosing dark lines radiating from the point of style attachment, as well as a diagnostic shape (Fig. 17b). Persistent styles (Fig. 17j) which usually were unattached, were shorter than those of *R. strigosus*.





*Geocaulon lividum*. The brilliant red-orange "skin" (exocarp) of the drupe was usually found in the pyloric region of the stomach, since it was eaten first. The "flesh" (mesocarp) was usually found segregated in the more anterior part of the stomach. This was a little paler than the "skin" and of a coarse consistency. Parts of the stone (endocarp) were seldom found and were never used diagnostically.

*Mitella nuda*. The tiny black shiny seeds of this fruit were very seldom found.

*Ribes oxycanthoides*. The berry "flesh" was not diagnostic. The seeds, spatulate in outline, had dark ends and a slight longitudinal ridge (Fig. 17d).

*Rosa woodsii*. The pulp of this fruit was the same general color as *G. lividum*, but not as brilliant. Achene fragments were not diagnostic.

*Rubus acaulis*. The fruit had no diagnostic characters. Large seeds (Fig. 17f) were often not found whole, at which time they were not diagnostic. These differed from other seeds of this genus by being smaller than *R. chamaemorus* and lacking the characteristic seed coat pattern of *R. strigosus*.

*Rubus chamaemorus*. The fruit pulp was yellow in color. The slightly ridged seed (Fig. 17e) was seldom found whole, and was smoother than that of *R. strigosus*, and larger than that of *R. acaulis*.

*Rubus strigosus*. The fruit pulp was dark in color and indistinguishable from that of *F. virginiana*. The "seed coat" (endocarp) had a characteristic pattern of pits and ridges (Fig. 17a). Persistent styles (Fig. 17j) (usually detached) were longer than those of *F. virginiana*.

*Shepherdia canadensis*. The fruit mass and large seed were not diagnostic. The ectocarp, however, had many attached and free stellate appendages (Fig. 17k) which were diagnostic.

*Vaccinium vitis-idaea*. The berry mass was characteristically reddish-violet and had less substance than *F. virginiana* and *R. strigosus*. Pieces of folded, transparent "skin" often accompanied the mass. The seeds (Fig. 17c) were redder than the flesh and were ovoid in shape with uneven curvature lengths. The seed surface had a wrinkled appearance.

Unidentified Fruit. All unidentifiable material which appeared to be fruit "flesh", mainly because of a light consistency, was placed in this category.





APPENDIX III

PHENOLOGICAL ADVENTS



The times of appearance of the various seasonal aspects of some important and conspicuous members of the flora. The blank spaces indicate inapplicability while the dashes mark a lack of data. Dates in parentheses are based on related observations. Abbreviations: MY, May; JN, June; JL, July; AG, August.

Species	New leaves	Flower buds	Flowers	Green fruits	Ripe fruits
<i>Geocaulon lividum</i>	-----	-----	JN 2/65	JL 8/65	JL25/65
	MY20/66	-----	JN 4/66	JL 1/66	JL23/66
	JN 4/67	-----	JN10/67	JL10/67	(AG 1/67)
	(JN 1/68)	-----	(JN 9/68)	-----	AG 3/68
<i>Rubus strigosus</i>	-----	-----	JN 6/65	-----	JL23/65
	-----	-----	JN 4/66	-----	JL20/66
	-----	JN 6/67	JN16/67	-----	(AG 2/67)
	-----	JN 4/68	JN14/68	-----	AG 1/68
<i>Fragaria virginiana</i>	-----	-----	MY31/65	-----	JL19/65
	-----	-----	MY29/66	JL 2/66	JL13/66
	-----	-----	JN 6/67	-----	(JL25/67)
	-----	-----	JN 5/68	-----	(JL25/68)
<i>Vaccinium vitis-idaea</i>		-----	(JN15/65)	-----	JL14/65
		-----	JN13/66	JN20/66	JL12/66
		JN 6/67	JN28/67	JL 4/67	(AG 1/67)
		-----	(JN25/68	-----	AG 2/68
<i>Arctostaphylos uva-ursi</i>		-----	-----	JL 9/65	-----
		MY18/66	MY23/66	JN28/66	JL18/66
		JN 1/67	JN 3/67	-----	(J130/67)
		-----	JN 4/68	-----	(JL30/68)
<i>Rosa woodsii</i>	JN 1/65	JN 8/65	JN14/65	-----	JL15/65
	-----	-----	JN13/66	-----	JL12/66
	(JN10/67)	-----	JN24/67	-----	(AG 5/67)
	JN12/68	-----	-----	(JL25/68)	AG 5/68
<i>Shepherdia canadensis</i>	-----	-----	-----	-----	JN30/65
	MY29/66	-----	MY14/66	JN26/66	JN30/66
	JN 6/67	-----	MY20/67	JL 4/67	JL 9/67
	JN 6/68	-----	-----	-----	(JL10/68)
<i>Ribes oxycanthoides</i>	-----	-----	JN 1/65	-----	JL15/65
	(MY15/66)	-----	MY25/66	JN14/66	JL23/66
	MY25/67	-----	JN 6/67	JL 4/67	AG 6/67
	-----	-----	-----	-----	(AG 1/68)



Species	New leaves	Flower buds	Flowers	Green fruits	Ripe fruits
	-----	-----	-----	-----	AG 4/65
<i>Rubus</i>	-----	-----	JN 6/66	-----	AG 6/66
<i>chamaemorus</i>	-----	-----	JN17/67	-----	(AG15/67)
	-----	-----	-----	-----	(AG13/68)
	JN 5/65	-----	JN 5/65	JN25/65	JL11/65
<i>Rubus</i>	-----	-----	JN 2/66	(JN15/66)	JL20/66
<i>acaulis</i>	-----	-----	JN15/67	JN30/67	(AG 1/67)
	-----	-----	-----	-----	AG 4/68
	-----	-----	-----	-----	JL11/65
<i>Arctostaphylos</i>	MY24/66	-----	MY24/66	(JL 1/66)	JL10/66
<i>rubra</i>	-----	-----	JN 6/67	-----	(JL20/67)
	-----	-----	-----	-----	-----
	-----	-----	JN19/65	-----	AG13/65
<i>Cornus</i>	-----	-----	JN13/66	-----	AG11/66
<i>canadensis</i>	MY20/67	-----	JN28/67	-----	(AG15/67)
	-----	-----	-----	-----	AG15/68
	JN 5/65	-----	JN 8/65	-----	-----
<i>Viburnum</i>	-----	-----	JN10/66	JL 2/66	JL21/66
<i>edule</i>	-----	-----	JN18/67	-----	(AG15/67)
	JN10/68	-----	-----	-----	(AG10/68)
		-----	-----	-----	-----
<i>Vaccinium</i>		-----	JN13/66	-----	JL28/66
<i>oxycoccus</i>		JN 6/67	JN25/67	-----	AG 8/67
		-----	-----	-----	AG 5/68
	-----	-----	-----	-----	-----
<i>Cornus</i>	-----	-----	JN15/66	-----	JL20/66
<i>stolonifera</i>	-----	-----	JN26/67	-----	AG10/67
	-----	-----	-----	-----	-----
	-----	-----	-----	-----	-----
<i>Mitella</i>	-----	-----	JN19/66	-----	-----
<i>nuda</i>	-----	-----	-----	-----	(JL10/67)
	-----	-----	-----	-----	-----
		-----	-----	JL11/65	JL19/65
<i>Empetrum</i>		MY25/66	MY29/66	-----	JL18/66
<i>nigrum</i>		JN 1/67	JN 7/67	-----	(AG 1/67)
		-----	-----	-----	-----





Species	New leaves	Flower buds	Flowers	Green fruits	Ripe fruits
<i>Linnaea borealis</i>	-----	-----	-----	-----	JL24/65
	-----	JN19/66	JN28/66	-----	JL16/66
	-----	-----	JL 5/67	-----	-----
	-----	-----	-----	-----	-----
<i>Populus tremuloides</i>	MY21/65	-----	-----	-----	-----
	MY20/66	-----	-----	-----	-----
	MY29/67	-----	-----	-----	-----
	-----	-----	-----	-----	-----
<i>Ledum groenlandicum</i>		-----	JN15/65	-----	JL14/65
		MY24/66	JN 9/66	-----	JL12/66
		JN 1/67	JN17/67	-----	(JL19/67
		-----	-----	-----	-----
<i>Ledum decumbens</i>		-----	JN 5/65	-----	JL 2/65
		-----	MY29/66	-----	-----
		JN 1/67	JN10/67	-----	(JL12/67)
		-----	-----	-----	-----
<i>Juniperus communis</i>				-----	-----
				JL 2/66	JL 6/66
				-----	JL28/67
				-----	-----
<i>Juniperus horizontalis</i>				-----	-----
				-----	JL 5/66
				-----	AG 1/67
				-----	-----
<i>Potentilla fruticosa</i>	-----	-----	JN18/65	-----	-----
	-----	-----	JN18/66	-----	-----
	-----	-----	JN27/67	-----	-----
	-----	-----	-----	-----	-----
<i>Epilobium angustifolium</i>	-----	JN15/65	JN24/65	-----	-----
	-----	-----	JN26/66	-----	-----
	-----	-----	JL 4/67	-----	-----
	-----	-----	-----	-----	-----
<i>Pyrola asarifolia</i>	JN 3/65	JN 5/65	JN15/65	-----	-----
	MY11/66	MY24/66	JN 9/66	-----	JL13/66
	MY25/67	JN 6/67	JN26/67	-----	JL27/67
	-----	-----	-----	-----	-----



APPENDIX IV

QUANTITATIVE DESCRIPTIONS OF THE  
BIOTOPES STUDIED



Stem number and dry weight per millacre of the members of the subsidiary flora in the white spruce and poplar forests. All values are averages of 20 estimates; amounts less than 0.1 gm are recorded as traces.

Species	White spruce				Poplar			
	C.r. area		C.g. area		C.r. area		C.g. area	
	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)
<i>Amelanchier alnifolia</i>					1.2	2.4		
<i>Cornus stolonifera</i>	tr	tr						
<i>Shepherdia canadensis</i>	2.6	23.6	0.4	1.4	5.8	34.8	26.5	689.0
<i>Virburnum edule</i>	2.1	5.5	tr	tr	9.1	2.7	5.1	35.7
<i>Rosa woodsii</i>	9.0	12.7	2.4	1.2	25.9	62.3	56.8	136.3
<i>Juniperus communis</i>					1.1	3.1	3.8	10.8
<i>J. horizontalis</i>							1.1	9.4
<i>Ribes oxycanthoides</i>	0.5	0.2						
<i>Ribes triste</i>	0.5	0.3						
<i>Epilobium angustifolium</i>	3.7	2.8			0.3	0.2	0.9	0.6
<i>Lathyrus ochroleucus</i>	0.7	0.3					0.5	0.2
<i>Vicia americana</i>	0.7	0.1					tr	tr
<i>Geocaulon lividum</i>	25.0	3.5	1.0	0.1	37.3	4.1		
<i>Pyrola asarifolia</i>	16.3	2.2	1.1	0.5	5.4	2.7	2.0	1.0
<i>P. secunda</i>	5.0	0.5	1.7	0.2	0.5	0.1	6.8	0.7
<i>Moneses uniflora</i>	4.0	0.2						





Species	White spruce (cont'd)				Poplar (Cont'd)			
	C.r. area		C.g. area		C.r. area		C.g. area	
	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)
<i>Equisetum scirpoides</i>	10.6	0.1	12.3	0.2				
<i>Fragaria virginiana</i>	14.1	0.4					0.5	tr
<i>Rubus acaulis</i>	7.7	0.3						
<i>Arctostaphylos uva-ursi</i>					22.8	18.2	20.6	16.5
<i>A. rubra</i>	1.2	0.6	0.1	tr				
<i>Linnaea borealis</i>	43.3	32.6	3.5	0.4	166.2	33.2	15.8	3.2
<i>Cornus canadensis</i>	37.6	4.4	0.9	tr			8.2	0.4
<i>Mitella nuda</i>	56.5	0.8						
Graminoids	16.2	1.5	3.0	0.3	150.5	30.1	123.0	24.6
Other shrubs and herbs <sup>1</sup>	0.2	0.4					1.5	0.2
<i>Peltigera</i> spp. <sup>2</sup>	8.2	3.8	0.4	0.2				
<i>Cladonia</i> spp. <sup>3</sup>	tr	0.7	0.3	9.0				
Feather moss <sup>4,5</sup>	64.8	896.5	7.8	694.2	0.4	38.7	0.2	17.8
Other mosses <sup>5</sup>	0.2	3.7			0.4	15.9	tr	tr

<sup>1</sup>Trace amounts of *Alnus* sp., *Salix* spp., *Galium boreale*, *Actaea rubra*, composites, *Habenaria* spp., *Equisetum arvense*.

<sup>2</sup>"Pieces" rather than stem number counted <sup>4</sup>Mostly *Hylocomium splendens*

<sup>3</sup>Some *Cetraria* sp. <sup>5</sup>Square footage rather than stem number estimated.



Stem number and dry weight per millacre of the members of the subsidiary flora in the black spruce forests.  
 All values are averages of 20 estimates; amounts less than 0.1 gm are recorded as traces.

Species	Immature black spruce				Mature black spruce			
	C.r. area	Dry wt. (gm)	Stem no.	C.g. area	C.r. area	Dry wt. (gm)	Stem no.	C.g. area
<i>Viburnum edule</i>					0.1	0.7		
<i>Rosa woodsii</i>	tr	tr			20.0	23.4		
<i>Potentilla fruticosa</i>	3.6	7.2		0.3	0.6			
<i>Juniperus communis</i>				0.9	2.3			
<i>J. horizontalis</i>				6.8	58.1			
<i>Ledum groenlandicum</i>	43.9	134.2		63.0	195.3	69.7	224.4	
<i>L. decumbens</i>	9.4	16.0		23.9	40.7	6.6	4.0	
<i>Epilobium angustifolium</i>	21.6	0.7						
<i>Chamaedaphne calyculata</i>	61.9	5.2		7.1	0.7			
<i>Andromeda polifolia</i>	51.2	5.6		59.9	6.0			
<i>Geocaulon lividum</i>	13.0	1.3		24.4	2.2	1.4	17.5	
<i>Equisetum arvense</i>	21.6	0.7		8.3	0.3	tr	0.2	
<i>E. scirpoides</i>	271.4	3.9		153.9	2.2	0.2	10.0	
<i>Empetrum nigrum</i>	41.7	75.1		47.6	85.7	13.1	7.4	
<i>Vaccinium vitis-idaea</i>	125.6	12.6		91.0	9.1	226.4	1741.5	
<i>V. oxycoccus</i>	85.0	1.7		136.8	1.4			
<i>Rubus acaulis</i>	1.8	0.1						



Species	Immature black spruce (Cont'd)				Mature black spruce (Cont'd)			
	C.r. area		C.g. area		C.r. area		C.g. area	
	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)
<i>R. chamaemorus</i>	0.3	tr						
<i>Arctostaphylos rubra</i>	21.9	4.4	11.4	2.3				
<i>Linnaea borealis</i>	3.0	0.6	3.1	0.6				
<i>Pinguicula vulgaris</i>	6.5	2.6	1.7	tr				
<i>Drosera rotundifolia</i>	20.5	8.2	35.9	10.0				
Other shrubs and herbs <sup>1</sup>	tr	tr	tr	tr	tr	tr		
Graminoids <sup>2</sup>	400.6	80.1	92.8	18.6	0.6	tr		
<i>Peltigera</i> spp.					119.8	44.3		
<i>Cladonia</i> spp. <sup>3</sup>	9.8	294.0	17.0	508.8	8.2	263.6		
Feather moss	0.7	63.0	tr	tr	2.7	69.7		
<i>Sphagnum</i> spp.	12.3	147.6	16.1	144.9	tr	tr		
Other mosses	6.8	247.8	1.3	48.5	13.8	215.4		

<sup>1</sup>Young *Picea mariana*, *Arctostaphylos uva-ursi*, *Ribes* sp., *Shepherdia canadensis* and *Spiranthes romanzoffiana*.

<sup>2</sup>Includes *Eriophorum* sp. only in the immature stands.

<sup>3</sup>Some *Cetraria* sp.





Stem number and dry weight per millacre of the members of the subsidiary flora in the jackpine forests. All values are averages of 20 estimates; amounts less than 0.1 gm are recorded as traces.

Species	Jackpine-juniper				Parklike jackpine			
	C.r. area		C.g. area		C.r. area		C.g. area	
	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)
<i>Cornus stolonifera</i>	1.1	0.1						
<i>Shepherdia canadensis</i>	6.0	22.0	1.0	13.6	5.1	30.3	6.0	5.1
<i>Virburnum edule</i>			0.1	tr	1.2	6.0	0.5	0.5
<i>Rosa woodsii</i>	19.0	4.5	22.3	6.7	22.6	55.0	6.7	14.7
<i>Potentilla fruticosa</i>	12.0	23.9			tr	tr		
<i>Juniperus communis</i>	4.0	10.6	6.6	28.6	tr	tr	tr	tr
<i>J. horizontalis</i>	4.6	33.8	0.4	3.0				
<i>Epilobium angustifolium</i>	3.0	0.2						
<i>Galium boreale</i>	6.6	0.6	0.1	0.1	4.8	0.5	tr	tr
<i>Pyrola asarifolia</i>	1.2	1.0					1.0	0.3
<i>P. secunda</i>			11.9	1.2	tr	tr	0.8	0.1
<i>Fragaria virginiana</i>	1.6	0.3	2.5	0.3				
<i>Empetrum nigrum</i>	0.6	5.2					tr	tr
<i>Vaccinium vitis-idaea</i>	41.1	4.5	tr	tr	tr	tr	174.5	34.9
<i>Arctostaphylos uva-ursi</i>	290.2	177.0	98.0	156.1	715.4	572.3	256.1	163.9
<i>A. rubra</i>	2.2	0.5						



Species	Jackpine-juniper (Cont'd)				Parklike jackpine (Cont'd)			
	C.r. area		C.g. area		C.r. area		C.g. area	
	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)	Stem no.	Dry wt. (gm)
<i>Linnaea borealis</i>	175.4	15.0	88.0	17.2	92.0	18.4	117.4	14.4
<i>Cornus canadensis</i>	tr	tr						
Graminoids	228.8	33.3	52.4	9.7	34.0	4.6	32.0	6.4
Other shrubs and herbs <sup>1</sup>			3.7	0.2	2.8	0.4		
<i>Peltigera</i> spp.	10.6	1.5	tr	tr			7.2	2.9
<i>Cladonia</i> spp. <sup>2</sup>	7.8	904.0	3.8	190.5	8.8	264.0	8.5	212.4
Feather moss	0.2	24.0	1.5	33.8	0.4	36.0	0.6	10.0
Other mosses	6.3	34.6	1.8	65.7			0.4	14.4

<sup>1</sup>*Amelanchier alnifolia*, composites, *Calypso bulbosa*, *Vicia americana* and *Campanula rotundifolia*.

<sup>2</sup>Some *Cetraria* spp.



APPENDIX V

RAW PERCENTAGES OF STOMACH CONTENTS (BASIC REGIMENS)





Raw percentage averages from which the consumption regimen of *P. maniculatus* in Fig. 29 was drawn. Each month is divided into four equal sections.

Time Mo   S		Number	Arthropods	Mushrooms	Achlorophyllous parts	Leaf	Fruits								Unidentified
							<i>R. woodsi</i>	<i>A. uva-ursi</i>	<i>V. vitis-idaea</i>	<i>G. lividum</i>	<i>R. strigosus</i>	<i>F. virginiana</i>	<i>S. canadensis</i>	Unidentified; Others	
4	3	5	23	0	1	0	21	10	1	0	0	0	0	34	11
	4	1	40	0	0	10	0	0	0	0	0	0	0	0	50
5	1	22	80	0	2	1	8	4	0	0	0	0	0	2	5
	2	16	60	0	0	0	6	14	0	0	0	0	0	19	7
	3	24	57	0	2	10	5	5	2	0	0	0	0	8	11
	4	38	61	0	0	2	11	3	6	0	0	0	0	7	10
6	1	19	64	0	1	1	<1	2	13	0	0	0	0	19	0
	2	38	83	0	0	5	2	3	4	0	0	0	0	3	0
	3	28	81	0	<1	1	0	3	3	0	0	0	1	2	9
	4	52	88	0	0	1	0	2	1	0	0	0	<1	3	4
7	1	45	84	0	0	<1	2	3	0	3	0	3	1	2	2
	2	36	78	0	0	<1	0	0	2	6	0	6	2	2	4
	3	59	49	0	0	1	2	4	2	7	10	3	7	4	9
	4	62	33	0	0	0	0	0	1	22	14	31	2	7	20
8	1	81	14	8	0	0	0	0	0	29	13	27	<1	4	5
	2	45	29	3	0	1	0	3	0	35	12	13	1	0	3
	3	55	12	0	0	0	0	0	2	33	26	21	<1	4	2
	4	48	14	1	0	8	1	4	1	30	19	10	5	9	8
9	1	3	42	0	0	0	1	0	4	31	5	0	0	15	12
10	1	2	50	0	3	0	0	0	10	0	0	0	0	25	13
	2	8	10	0	15	4	8	6	29	0	0	0	11	7	10



Raw percentage averages from which the consumption regimen of *C. rutilus* in Fig. 29 was drawn. Each month is divided into four equal sections.

Mo	Time S	Number	Mushrooms	<i>Parmelia</i> spp.	<i>Usnea</i> sp.	<i>A. jubata</i>	Achlorophyllous parts	Leaf	Fruits								Unidentified; Others	Unidentified
									<i>R. woodsi</i>	<i>A. uva-ursi</i>	<i>V. vitis-idaea</i>	<i>G. lividum</i>	<i>R. strigosus</i>	<i>F. virginiana</i>	<i>S. canadensis</i>			
1	1	9	0	14	0	4	0	5	2	0	34	0	0	0	0	0	41	
2	4	10	0	7	3	13	1	3	20	3	47	0	0	0	0	0	3	
3	3	4	0	42	5	13	3	0	0	16	0	0	0	0	0	0	21	
4	1	6	0	18	3	7	0	0	17	0	22	0	0	0	0	0	33	
5	2	1	0	0	0	0	0	50	0	0	50	0	0	0	0	0	0	
	3	20	1	13	0	7	0	11	0	0	40	0	0	0	0	5	15	
	4	9	0	0	0	2	0	24	0	0	57	0	0	0	0	17	0	
6	1	3	0	5	0	10	0	48	1	0	13	0	0	0	0	23	0	
	2	5	3	0	0	1	1	36	0	1	34	0	0	0	0	14	10	
	3	11	0	13	0	12	0	28	0	0	33	0	0	0	0	10	4	
	4	15	9	6	0	4	0	38	0	0	17	0	0	0	1	25	15	
7	1	12	0	9	0	6	0	24	1	1	18	2	0	2	0	18	6	
	2	11	34	2	0	4	<1	11	0	0	37	0	0	0	0	8	4	
	3	2	25	0	0	0	0	3	0	0	0	5	0	0	0	25	42	
8	1	16	50	0	0	0	0	<1	5	4	6	3	6	5	0	3	17	
	2	10	40	0	0	0	0	0	0	0	0	21	5	5	0	0	29	
	3	6	68	0	0	0	0	0	0	0	0	15	0	0	0	0	17	
	4	20	46	0	0	0	<1	1	0	0	5	21	3	0	6	13	5	
9	1	4	34	0	0	0	0	0	0	0	0	50	0	0	0	0	16	
10	1	3	4	3	0	0	0	4	2	1	60	0	0	0	0	13	13	
	2	16	13	26	11	3	6	5	0	0	0	5	0	0	0	10	19	
	3	9	3	0	0	10	1	0	0	0	69	0	0	0	0	9	8	
11	2	15	0	34	15	13	3	1	1	2	15	0	0	0	0	3	13	
12	2	1	3	0	0	10	0	0	0	0	90	0	0	0	0	0	0	









APPENDIX VI

RAW PERCENTAGES OF STOMACH CONTENTS (ANNUAL COMPARISONS)



Raw percentage averages from which the consumption regimens of *P. maniculatus* for 1965 and 1966 (Fig. 29) were constructed. Results are indicated chronologically for the monthly quarter in which they were obtained.

Time Mo   Q	Number	Arthropods	Mushrooms	Achlorophyllous parts	Leaf	Fruits								Unidentified Others	Unidentified
						<i>R. woodsii</i>	<i>A. uva-ursi</i>	<i>V. vitis-idaea</i>	<i>G. lividum</i>	<i>R. strigosus</i>	<i>F. virginiana</i>	<i>S. canadensis</i>			
1965															
5 3	5	33	0	2	13	14	20	0	0	0	0	0	18	0	
4	11	71	0	5	6	2	5	0	0	0	0	0	11	0	
6 1	10	82	0	0	0	1	6	0	0	0	0	0	6	5	
2	19	81	0	0	1	10	0	0	0	0	0	0	8	0	
3	17	80	0	5	3	0	4	0	0	0	0	0	0	8	
4	31	84	0	0	3	2	3	0	0	0	0	0	2	6	
7 1	17	75	0	0	1	7	0	5	0	0	0	1	4	7	
2	15	88	0	0	0	0	0	0	2	0	2	5	0	3	
3	20	60	0	0	0	2	5	0	7	6	3	5	6	6	
4	9	42	0	0	3	0	0	1	28	15	10	0	2	0	
8 1	11	15	13	0	0	0	0	0	24	9	23	0	10	7	
2	14	15	4	0	0	0	13	0	42	8	8	2	4	4	
3	4	14	0	0	4	0	4	0	20	15	30	0	0	13	
4	2	15	0	5	15	0	2	0	0	8	9	7	19	9	
1966															
5 4	6	24	0	1	1	31	3	8	0	0	0	0	14	18	
6 2	5	86	0	0	0	10	4	0	0	0	0	0	0	0	
3	4	54	0	0	12	9	8	0	0	0	0	0	0	17	
4	13	85	0	0	0	7	0	0	0	0	0	1	0	7	
7 1	26	58	0	<1	1	<1	0	3	10	0	8	1	12	6	
2	18	55	0	0	1	0	0	5	2	0	16	6	4	11	
3	33	39	0	2	<1	2	1	3	14	5	9	15	5	5	
4	47	40	0	0	0	0	4	1	16	13	20	4	0	3	
8 1	55	22	0	<1	1	<1	0	1	30	27	8	1	2	6	
2	24	22	4	0	0	<1	0	2	40	8	12	0	4	8	
3	35	10	0	0	<1	0	0	3	49	36	2	2	5	3	
4	26	21	0	0	<1	0	0	9	39	19	2	1	2	7	
9 1	3	63	0	0	0	0	0	4	0	33	0	0	0	0	



Raw percentage averages from which the consumption regimens of *P. maniculatus* for 1967 and 1968 (Fig. 29) were constructed. Results are indicated chronologically for the monthly quarter in which they were obtained.

Mo	Time Q	Number	Arthropods	Mushrooms	Achlorophyllous parts	Leaf	Fruits								Unidentified
							<i>R. woodsii</i>	<i>A. uva-ursi</i>	<i>V. vitis-idaea</i>	<i>G. Lividum</i>	<i>R. strigosus</i>	<i>F. virginiana</i>	<i>S. canadensis</i>	Unidentified; Others	
1967															
5	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	4	72	0	0	12	0	0	4	0	0	0	0	12	0
	4	21	91	0	0	1	0	5	10	0	0	0	0	2	1
6	1	7	99	0	1	0	0	0	0	0	0	0	0	0	0
	2	7	100	0	0	0	0	0	0	0	0	0	0	0	0
	3	7	80	0	0	4	0	0	16	0	0	0	0	0	0
	4	7	90	0	0	0	8	0	0	0	0	0	0	0	2
7	1	2	50	0	0	2	0	0	0	0	0	0	0	0	48
	2	3	100	0	0	0	0	0	0	0	0	0	0	0	0
	3	6	52	0	0	2	15	3	2	0	0	0	2	0	14
8	3	4	6	0	0	0	0	0	5	20	25	14	5	0	25
	4	20	8	4	0	0	3	0	5	12	29	27	13	3	6
1968															
5	2	11	43	0	0	0	0	38	0	0	0	0	0	6	13
	3	15	48	0	2	8	0	12	0	0	0	0	0	20	10
6	1	2	10	0	0	0	0	11	20	0	0	0	0	50	9
	2	7	87	0	0	3	0	2	0	0	0	0	0	0	8
	4	1	100	0	0	0	0	0	0	0	0	0	0	0	0
7	4	6	18	0	0	0	0	0	0	9	0	32	4	0	37
8	1	14	12	2	0	0	0	0	1	32	4	30	6	0	10
	2	7	43	0	0	0	0	0	0	11	21	20	0	0	5
	3	12	12	0	0	2	0	0	0	12	28	27	0	0	7





Raw percentage averages from which the consumption regimens of *C. rutilus* 1965 to 1968 inclusive (Fig. 29) were constructed. Results are indicated chronologically for the monthly quarter in which they were obtained.

Time Mo   Q		Number	Mushrooms	<i>Parmelia</i> spp.	<i>A. jubata</i>	Achlorophyllous parts	Leaf	Fruits								Unidentified
								<i>R. woodsii</i>	<i>A. uva-ursi</i>	<i>V. vitis-idaea</i>	<i>G. lividum</i>	<i>R. strigosus</i>	<i>F. virginiana</i>	<i>S. canadensis</i>	Unidentified; Others	
1965																
5	4	6	0	6	1	0	41	0	0	16	0	0	0	0	18	18
6	1	2	0	0	0	0	40	0	0	15	0	0	0	0	25	20
	2	1	0	0	0	0	60	0	0	0	0	0	0	0	0	40
	3	3	0	3	7	0	60	0	0	0	0	0	0	0	0	30
	4	15	9	0	4	6	17	0	0	12	0	0	0	0	37	15
7	1	3	0	8	8	0	37	0	0	0	0	0	0	0	47	0
	2	8	24	0	4	1	11	0	0	44	0	0	3	0	0	13
	3	2	25	0	0	0	3	0	0	0	5	0	0	1	25	42
8	1	9	27	0	0	0	0	7	0	8	39	6	8	0	0	5
	2	3	67	0	0	0	0	0	0	0	33	0	0	0	0	0
9	1	1	60	0	0	0	0	0	0	7	0	0	0	7	11	15
1966																
6	3	5	0	6	3	1	36	0	0	10	0	0	0	0	21	23
7	1	9	6	1	3	0	18	0	0	36	0	0	0	0	12	15
	2	3	24	3	3	0	6	0	2	30	7	0	10	4	0	9
8	1	7	29	0	0	0	1	0	3	6	15	7	5	8	0	26
	2	6	18	0	0	0	0	0	0	0	65	14	4	3	0	9
	3	5	9	0	0	1	2	0	0	0	47	12	4	6	0	19
9	1	3	67	0	0	0	0	0	0	0	4	0	0	10	3	16
1967																
5	3	10	0	2	5	2	18	0	0	67	0	0	0	0	0	6
	4	3	6	3	0	0	0	0	0	91	0	0	0	0	0	0
6	2	4	5	0	2	0	0	0	0	68	0	0	0	0	0	25
	3	3	0	0	0	0	0	0	0	100	0	0	0	0	0	0
7	4	20	54	0	0	1	1	0	0	20	13	0	0	6	5	0
1968																
5	3	10	0	17	16	1	24	0	0	18	0	0	0	0	11	13
6	1	1	0	0	20	0	70	0	0	10	0	0	0	0	0	0
8	2	1	90	0	0	0	0	0	0	0	0	0	0	0	0	10
	3	1	50	0	0	0	0	0	0	0	17	0	0	0	0	33



Raw percentage averages from which the consumption regimens of *C. gapperi* for 1965 and 1966 (Fig. 29) were constructed. Results are indicated chronologically for the monthly quarter in which they were obtained.

Time Mo   Q		Number	Mushrooms	<i>Parmelia</i> spp.	<i>A. jubata</i>	Achlorophyllous parts	Leaf	Fruits								Unidentified	
								<i>R. woodsii</i>	<i>A. uva-ursi</i>	<i>V. vitis-idaea</i>	<i>G. lividum</i>	<i>R. strigosus</i>	<i>F. virginiana</i>	<i>S. canadensis</i>	Unidentified; Others		
1965																	
5	4	1	0	20	5	0	20	0	0	15	0	0	0	0	20	20	
6	3	1	0	10	0	0	30	0	0	0	0	0	0	0	0	60	
7	2	1	20	0	0	0	10	0	0	0	0	0	70	0	0	0	
	4	1	0	0	0	0	100	0	0	0	0	0	0	0	0	0	
8	1	4	30	0	0	0	2	10	0	12	11	20	0	8	0	7	
	2	3	33	0	0	1	4	0	0	0	30	7	2	6	0	17	
	4	4	63	0	0	0	0	0	0	0	18	6	13	0	0	0	
9	1	3	0	0	0	0	0	0	27	0	19	0	20	0	0	34	
1966																	
5	4	1	0	50	30	0	10	0	0	0	0	0	0	0	0	10	
6	3	6	0	1	7	0	30	0	0	2	0	0	0	0	18	42	
	4	6	4	28	4	0	11	0	0	0	3	0	15	10	12	13	
7	1	5	0	17	11	0	26	0	0	0	4	0	2	8	15	15	
	2	4	25	17	5	0	0	0	0	0	0	0	26	0	10	17	
	3	16	13	11	7	2	2	0	0	5	8	1	5	20	2	24	
	4	24	38	7	2	0	8	0	0	5	3	12	4	11	0	12	
8	1	28	28	4	2	0	3	0	0	6	9	17	4	12	0	15	
	2	11	14	1	<1	0	1	0	0	0	18	29	2	11	0	13	
	3	18	8	0	0	0	4	0	0	0	40	22	1	12	0	15	
	4	12	0	0	<1	2	0	0	0	0	57	0	4	0	0	23	
9	1	3	66	0	0	0	0	0	0	0	33	0	0	0	0	0	



Raw percentage averages from which the consumption regimens of *C. gapperi* for 1967 and 1968 (Fig. 29) were constructed. Results are indicated chronologically for the monthly quarter in which they were obtained.

Time Mo   Q		Number	Mushrooms	<i>Parmelia</i> spp.	<i>A. jubata</i>	Achlorophyllous parts	Leaf	Fruits								Unidentified	
								<i>R. woodsii</i>	<i>A. uva-ursi</i>	<i>V. vitis-idaea</i>	<i>G. lividum</i>	<i>R. strigosus</i>	<i>F. virginiana</i>	<i>S. canadensis</i>	Unidentified; Others		
1967																	
5	2	1	0	0	10	0	0	0	0	70	0	0	0	0	0	20	
	3	4	0	10	2	32	0	0	27	12	0	0	0	0	10	7	
	4	4	0	5	20	1	36	0	0	40	0	0	0	0	0	0	
6	1	7	0	9	9	0	60	0	0	14	0	0	0	0	0	8	
	2	3	10	0	0	4	62	0	0	4	0	0	0	0	8	12	
	3	1	0	40	10	0	0	0	0	0	0	0	0	0	0	50	
	4	6	17	3	5	0	42	0	0	10	0	0	0	0	0	20	
7	1	2	60	7	0	0	3	0	0	10	5	0	0	0	0	15	
	2	3	67	3	2	0	7	0	0	0	0	0	0	0	20	0	
	3	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	
	4	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	
8	3	2	20	0	0	1	7	2	0	0	25	0	0	36	9	0	
	4	5	40	0	0	0	0	0	5	0	25	0	0	6	0	23	
1968																	
5	2	1	0	0	20	0	10	0	0	0	0	0	0	0	0	70	
	3	1	0	10	15	0	50	0	0	0	0	0	0	0	10	75	
	4	1	0	0	0	0	0	0	0	100	0	0	0	0	0	0	
6	1	3	0	25	12	0	43	0	0	20	0	0	0	0	0	0	
	2	3	0	7	0	0	81	7	0	2	0	0	0	0	0	3	
7	4	4	52	3	0	0	0	11	0	2	2	0	0	0	0	30	
8	1	6	70	0	1	0	0	2	0	0	1	0	0	0	0	26	
	2	2	80	0	0	0	0	0	0	0	0	0	0	1	2	17	
	3	1	80	0	0	0	0	0	0	3	5	0	2	0	0	10	





APPENDIX VII

FREQUENCY OF OCCURRENCE OF STOMACH CONTENTS  
(BASIC REGIMENS)



The frequency of occurrence of identified foods among the stomach contents expressed as percentages in whole numbers. A dash indicates that the food was not available during a particular period. Sample numbers are shown in parentheses under the first item. Juvenile stomachs, which showed no sexual differences, are combined in the fruiting period.

Food	Species	Age	Sex	Period					
				Vernal <sup>1</sup>		Fruiting <sup>2</sup>		Winter	
Arthropods	<i>P.m.</i>	Ad.	M	87	(134)	68	(84)	46	(20)
			F	100	(102)	83	(66)	45	(14)
		Juv.	M&F			71	(294)		
	<i>C.r.</i>	Ad.	M	7	(43)	5	(37)	1	(47)
			F	20	(30)	2	(21)	3	(34)
		Juv.	M&F			3	(26)		
	<i>C.g.</i>	Ad.	M	2	(45)	5	(63)	4	(42)
			F	20	(26)	7	(60)	1	(18)
		Juv.	M&F			3	(38)		
Mushrooms	<i>P.m.</i>	Ad.	M	0		3		0	
			F	0		2		0	
		Juv.	M&F			2			
	<i>C.r.</i>	Ad.	M	7		37		4	
			F	8		62		10	
		Juv.	M&F			41			
	<i>C.g.</i>	Ad.	M	4		42		7	
			F	0		35		0	
		Juv.	M&F			32			
<i>Parmelia</i> spp.	<i>P.m.</i>	Ad.	M	0		0		0	
			F	0		0		0	
		Juv.	M&F			1			
	<i>C.r.</i>	Ad.	M	7		3		31	
			F	12		0		26	
		Juv.	M&F			0			
	<i>C.g.</i>	Ad.	M	30		6		37	
			F	40		17		29	
		Juv.	M&F			8			
<i>Usnea</i> sp.	<i>P.m.</i>	Ad.	M	0		0		0	
			F	0		0		0	
		Juv.	M&F			0			
	<i>C.r.</i>	Ad.	M	2		0		11	
			F	0		0		26	
		Juv.	M&F			0			
	<i>C.g.</i>	Ad.	M	0		0		20	
			F	8		0		12	
		Juv.	M&F			0			

<sup>1</sup>May, June and the first week of July.

<sup>2</sup>Remainder of July and August.



(Cont'd)

Food	Species	Age	Sex	Period		
				Vernal <sup>1</sup>	Fruiting <sup>2</sup>	Winter
<i>A. jubata</i>	<i>P.m.</i>	Ad.	M	0	0	0
			F	1	2	0
		Juv.	M&F		1	
	<i>C.r.</i>	Ad.	M	29	8	53
			F	36	6	55
		Juv.	M&F		7	
	<i>C.g.</i>	Ad.	M	69	11	61
			F	64	20	65
		Juv.	M&F		8	
Feather mosses	<i>P.m.</i>	Ad.	M	5	2	15
			F	4	1	99
		Juv.	M&F		2	
	<i>C.r.</i>	Ad.	M	7	0	4
			F	8	3	7
		Juv.	M&F		6	
	<i>C.g.</i>	Ad.	M	2	7	7
			F	8	10	6
		Juv.	M&F		5	
Leaf	<i>P.m.</i>	Ad.	M	13	11	15
			F	9	6	9
		Juv.	M&F		7	
	<i>C.r.</i>	Ad.	M	35	11	20
			F	40	6	20
		Juv.	M&F		14	
	<i>C.g.</i>	Ad.	M	48	14	20
			F	56	17	12
		Juv.	M&F		11	
<i>R. woodsii</i> fruits	<i>P.m.</i>	Ad.	M	6	8	8
			F	4	5	10
		Juv.	M&F		2	
	<i>C.r.</i>	Ad.	M	0	2	9
			F	8	0	7
		Juv.	M&F		0	
	<i>C.g.</i>	Ad.	M	0	5	6
			F	4	2	10
		Juv.	M&F		0	
<i>A. uva-ursi</i> fruits	<i>P.m.</i>	Ad.	M	10	0	8
			F	11	0	3
		Juv.	M&F		2	
	<i>C.r.</i>	Ad.	M	0	0	2
			F	2	4	0
		Juv.	M&F		0	
	<i>C.g.</i>	Ad.	M	7	2	2
			F	4	2	0
		Juv.	M&F		0	





(Cont'd)

Food	Species	Age	Sex	Period		
				Vernal <sup>1</sup>	Fruiting <sup>2</sup>	Winter
<i>V. vitis-idaea</i> fruits	<i>P.m.</i>	Ad.	M	5	5	15
			F	4	11	27
		Juv.	M&F		4	
	<i>C.r.</i>	Ad.	M	45	26	27
			F	32	19	16
		Juv.	M&F		17	
	<i>C.g.</i>	Ad.	M	20	6	10
			F	12	3	35
		Juv.	M&F		5	
<i>G. lividum</i> fruits	<i>P.m.</i>	Ad.	M	--	38	10
			F	--	33	10
		Juv.	M&F		30	
	<i>C.r.</i>	Ad.	M	--	29	4
			F	--	25	3
		Juv.	M&F		21	
	<i>C.g.</i>	Ad.	M	--	13	0
			F	--	15	0
		Juv.	M&F		21	
<i>R. strigosus</i> fruits	<i>P.m.</i>	Ad.	M	--	30	3
			F	--	20	9
		Juv.	M&F		22	
	<i>C.r.</i>	Ad.	M		9	0
			F	--	0	0
		Juv.	M&F		4	
	<i>C.g.</i>	Ad.	M	--	13	0
			F	--	15	0
		Juv.	M&F		18	
<i>F. virginiana</i> fruits	<i>P.m.</i>	Ad.	M	--	26	0
			F	--	15	0
		Juv.	M&F		18	
	<i>C.r.</i>	Ad.	M	--	2	0
			F	--	12	0
		Juv.	M&F		0	
	<i>C.g.</i>	Ad.	M	--	13	0
			F	--	3	0
		Juv.	M&F		2	
<i>S. canadensis</i> fruits	<i>P.m.</i>	Ad.	M	--	4	7
			F	--	8	9
		Juv.	M&F		9	
	<i>C.r.</i>	Ad.	M	--	2	0
			F	--	6	0
		Juv.	M&F		0	
	<i>C.g.</i>	Ad.	M	--	13	2
			F	--	13	1
		Juv.	M&F		16	



APPENDIX VIII

FREQUENCY OF OCCURRENCE OF STOMACH CONTENTS  
(ANNUAL COMPARISONS)



The frequency of occurrence of identified foods among the stomach contents by year and season expressed as percentages. A dash indicates when the food was not available. Sample numbers are shown in parentheses under the first item.

Food	Species	Time									
		Vernal period 1965	Fruiting season 1965	Winter 1965-66	Vernal period 1966	Fruiting season 1966	Winter 1966-67	Vernal period 1967	Fruiting season 1967	Vernal period 1968	Fruiting season 1968
Insects	<i>P.m.</i>	99 (98)	90 (96)		100 (32)	71 (217)		93 (68)	50 (67)	83 (53)	51 (81)
	<i>C.r.</i>	14 (28)	0 (23)	6 (50)	14 (14)	0 (19)	0 (31)	5 (20)	0 (22)	19 (11)	0 (20)
	<i>C.g.</i>	9 (6)	0 (11)	3 (35)	10 (19)	3 (116)	3 (26)	0 (29)	0 (13)	7 (17)	0 (21)
Mushrooms	<i>P.m.</i>	1	3	-	0	1	-	0	3	0	0
	<i>C.r.</i>	7	30	-	0	20	-	10	50	0	57
	<i>C.g.</i>	11	38	-	0	7	-	6	44	0	32
<i>Parmelia</i> spp.	<i>P.m.</i>	0	0		0	0		0	0	0	0
	<i>C.r.</i>	5	0	41	15	12	10	9	0	21	0
	<i>C.g.</i>	40	9	29	63	11	23	0	0	18	14
<i>Usnea</i> sp.	<i>P.m.</i>	0	0		0	0		0	0	0	0
	<i>C.r.</i>	0	0	22	0	0	20	0	0	2	0
	<i>C.g.</i>	0	0	19	0	0	15	0	0	5	0
<i>A. jubata</i>	<i>P.m.</i>	0	2		0	0		5	0	0	2
	<i>C.r.</i>	42	19	59	15	0	30	34	3	29	2
	<i>C.g.</i>	37	19	57	30	23	58	55	8	37	10
Feather mosses	<i>P.m.</i>	5	5		4	0		7	0	3	2
	<i>C.r.</i>	7	0	8	0	1	5	0	0	26	5
	<i>C.g.</i>	3	3	6	5	6	8	0	2	15	5
Leaf	<i>P.m.</i>	12	10		8	3		14	12	15	8
	<i>C.r.</i>	63	9	22	30	10	19	5	7	54	8
	<i>C.g.</i>	40	20	19	55	2	14	53	23	50	27





Food	Species	Time									
		Vernal period 1965	Fruiting season 1965	Winter 1965-66	Vernal period 1966	Fruiting season 1966	Winter 1966-67	Vernal period 1967	Fruiting season 1967	Vernal period 1968	Fruiting season 1968
<i>R. woodsi</i> (fruits)	<i>P.m.</i>	8	7		11	8	0	9	5	3	7
	<i>C.r.</i>	3	2	7	2	0	10	0	0	8	0
	<i>C.g.</i>	0	2	6	0	2	7	0	0	6	5
<i>A. Uva-ursi</i> (fruits)	<i>P.m.</i>	4	2		10	2		6	3	35	0
	<i>C.r.</i>	0	0	2	0	0	0	0	0	1	1
	<i>C.g.</i>	0	0	3	5	1	0	7	4	0	3
<i>V. vitis-idaea</i> (fruits)	<i>P.m.</i>	0	9		4	6		14	14	3	3
	<i>C.r.</i>	9	27	2	29	15	45	90	26	3	30
	<i>C.g.</i>	14	19	14	15	5	14	23	0	17	0
<i>G. lividum</i> (fruits)	<i>P.m.</i>	-	25	-	-	39	-	-	33	-	30
	<i>C.r.</i>	-	26	-	-	30	-	-	26	-	35
	<i>C.g.</i>	-	14	-	-	18	-	-	19	-	14
<i>R. strigosus</i> (fruits)	<i>P.m.</i>	-	20	-	-	24	-	-	36	-	22
	<i>C.r.</i>	-	4	-	-	5	-	-	4	-	5
	<i>C.g.</i>	-	5	-	-	11	-	-	7	-	8
<i>F. virginiana</i> (fruits)	<i>P.m.</i>	-	14	-	-	20	-	-	33	-	37
	<i>C.r.</i>	-	5	-	-	5	-	-	5	-	5
	<i>C.g.</i>	-	8	-	-	8	-	-	2	-	3
<i>S. canadensis</i> (fruits)	<i>P.m.</i>	-	8	-	-	8	-	-	9	-	3
	<i>C.r.</i>	-	4	-	-	5	-	-	4	-	6
	<i>C.g.</i>	-	5	-	-	11	10	-	8	-	10



APPENDIX IX

FREQUENCY OF OCCURRENCE OF STOMACH CONTENTS  
(BIOTOPIC COMPARISONS)



The frequency of occurrence of identified foods among the stomach contents of *P. maniculatus* by biotope expressed as percentages. Sites from which fewer than ten stomachs were taken are arbitrarily omitted. Sample numbers are given in Figure 33. 1=white spruce; 2=poplar; 3=mature black spruce; 4=jackpine-juniper; 5=mixed forest; a=*C. rutilus* territory; b=*C. gapperi* territory.

Food		Vernal Period				Fruiting Period				
		1	2	4	5	1	2	3	4	5
Insects	a	98	79	100	75	56	40	98	67	80
	b			80	91	89	70		74	60
Mushroom	a	0	0	0	0	6	10	6	7	3
	b			0	0	0	10		60	0
<i>Parmelia</i> spp.	a	0	5	0	0	0	0	0	0	0
	b			0	0	0	0		2	0
<i>A. jubata</i>	a	0	0	0	0	0	0	0	0	0
	b			0	0	0	0		0	2
Feather mosses	a	3	0	5	5	3	0	0	0	1
	b			0	3	0	0		60	0
Leaf	a	5	0	10	22	7	7	2	0	10
	b			10	7	0	0		60	7
<i>R. woodsii</i> fruit	a	2	12	10	2	2	0	8	0	6
	b			0	3	0	0		60	1
<i>A. uva-ursi</i> fruit	a	5	0	15	2	2	0	0	0	2
	b			35	5	0	0		0	2
<i>V. vitis-idaea</i> fruit	a	0	18	5	0	2	0	20	13	6
	b			0	4	0	0		60	4
<i>G. lividum</i> fruit	a	-	-	-	-	25	70	57	40	24
	b	-	-	-	-	50	60		50	30
<i>R. strigosus</i> fruit	a	-	-	-	-	32	40	20	34	33
	b	-	-	-	-	79	30		20	28
<i>F. virginiana</i> fruit	a	-	-	-	-	48	30	26	53	11
	b	-	-	-	-	33	60		18	13
<i>S. canadensis</i> Fruit	a	-	-	-	-	7	5	2	0	6
	b	-	-	-	-	0	30		16	5





The frequency of occurrence of identified foods among the stomach contents of *Clethrionomys* spp. by biotope expressed as percentages. Sites from which fewer than ten stomachs were taken are arbitrarily omitted. Sample numbers are given in Figure 34. 1=white spruce; 2=poplar; 3=black spruce; 4=jackpine-juniper; 5=mixed forest; a=*C. rutilus* territory; b=*C. gapperi* territory.

Food		Vernal Period					Fruiting Period			
		1	2	3	4	5	1	3	4	5
Insects	a	22		0		5	7	0		10
	b		37		8	10	10		3	23
Mushrooms	a	14		0		0	60	23		50
	b		0		8	0	0		37	33
<i>Parmelia</i> spp.	a	11		0		11	0	0		5
	b		90		42	23	0		10	11
<i>A. jubata</i>	a	39		21		22	0	0		5
	b		100		75	50	10		23	20
Feather mosses	a	11		0		5	0	0		5
	b		10		0	7	0		13	7
Leaf	a	47		8		50	20	4		16
	b		40		25	73	20		23	13
<i>R. woodsii</i> fruit	a	6		0		0	0	5		0
	b		0		0	7	10		13	0
<i>A. uva-ursi</i> fruit	a	0		0		0	0	5		0
	b		0		25	0	0		7	0
<i>V. vitis-idaea</i> fruit	a	11		96		39	0	50		10
	b		0		0	23	0		7	6
<i>G. lividum</i> fruit	a	-	-	-	-	-	20	32		20
	b	-	-	-	-	-	10		17	21
<i>R. strigosus</i> fruit	a	-	-	-	-	-	0	10		0
	b	-	-	-	-	-	60		0	17
<i>F. virginiana</i> fruit	a	-	-	-	-	-	13	5		6
	b	-	-	-	-	-	20		0	8
<i>S. canadensis</i> fruit	a	-	-	-	-	-	7	5		0
	b	-	-	-	-	-	0		10	16



The frequency of occurrence of identified foods among the winter stomach contents of *Clethrionomys* spp. by biotope expressed as percentages. Sites from which fewer than ten stomachs were taken are arbitrarily omitted. Sample numbers are given in Figure 35. a=*C. rutilus*; b=*C. gapperi*.

Food		White Spruce	Black Spruce	Jackpine-juniper	Mixed Forest
Insects	a b	2	0	20	14 0
Mushrooms	a b	7	8	10	7 5
<i>Parmelia</i> spp.	a b	35	8	50	43 20
<i>Usnea</i> sp.	a b	18	0	0	36 25
<i>A. jubata</i>	a b	53	61	70	42 40
Feather mosses	a b	5	15	10	0 5
Leaf	a b	20	8	20	15 5
<i>R. woodsii</i> fruit	a b	15	0	0	0 10
<i>A. uva-ursi</i> fruit	a b	2	0	0	7 5
<i>V. vitis-idaea</i> fruit	a b	7	92	20	15 15





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